

Virginia Division of Mineral Resources  
Publication 152

**Early Eocene Vertebrates and Plants from the  
Fisher/Sullivan Site  
(Nanjemoy Formation) Stafford County, Virginia**

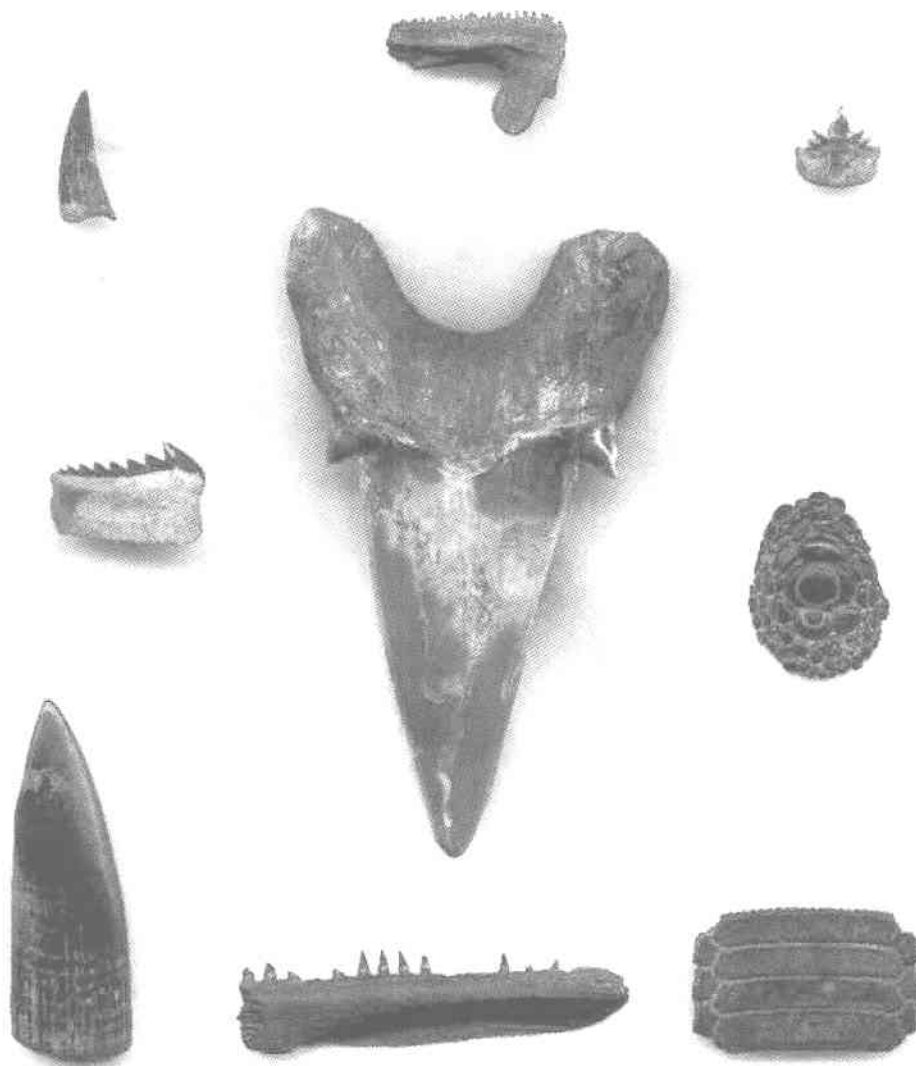


COMMONWEALTH OF VIRGINIA  
DEPARTMENT OF MINES, MINERALS AND ENERGY  
DIVISION OF MINERAL RESOURCES  
Stanley S. Johnson, State Geologist  
CHARLOTTESVILLE, VIRGINIA

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Front Cover: Selected vertebrate specimens from the Fisher/Sullivan site: Clockwise from upper left - crocodilian tooth (*Eosuchus lerichei*), sea bass upper jaw (*Cyclopoma folmeri*), cow shark lower symphyseal tooth (*Hexanchus* sp.), phyllodont bony-fish tooth plate (*Phyllodus toliapicus*), eagle ray lower dental pavement (*Myliobatis striatus*), mackerel lower jaw (*Scomberomorus stormsi*), sawfish rostral tooth (*Pristis lathamii*), cow shark lower lateral tooth (*Hexanchus* sp.). Center - giant mackerel shark lower anterior tooth (*Otodus obliquus*).

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Robert E. Weems and Gary J. Grimsley, Editors

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## PREFACE

The articles collected in this volume represent the culmination of many years of labor, both physical and intellectual, on the part of a great many people from many different walks of life. Through their common dedication to knowledge and enlightenment, these people have made it possible to produce an exceptionally focused and coherent picture of a part of prehistoric time, the early Eocene, that has been one of the least known and least understood portions of Virginia's prehistory. Thanks to the combined efforts of all of these people, for the first time we have a comprehensive picture of the fish and marine reptiles that lived in the coastal seas of Virginia 53 million years ago. Similarly, for the first time anywhere along the Atlantic Coast, we also can get a meaningful glimpse of the co-occurring plants, reptiles, birds, and mammals that inhabited the onshore coastal region.

Without the efforts of so many individuals at every stage of this study, the story that has unfolded would have been much less complete and informative. For this reason, those who are interested in the prehistory of the Commonwealth of Virginia owe thanks to each of these people for helping to save and interpret the remains that have been unearthed. The individuals who participated in specific stages of each part of this research generally are acknowledged, in one fashion or another, within each of the subsequent chapters. However, a more general word of thanks is due to the personnel of the Museum of Natural History in London, who generously made their specimens from the London Clay available for direct comparison and study. Similarly, Dr. Lynn Fichter of Madison College also deserves a special word of thanks for ably undertaking the massive task of reviewing all of the completed articles for the Virginia Division of Mineral Resources, both individually and collectively, for technical accuracy and mutual integration. Thanks to his efforts, this volume has been greatly improved and will be more easily understood by all who have occasion to use it.

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## PART 1. INTRODUCTION, GEOLOGY, AND PALEOGEOGRAPHIC SETTING

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### INTRODUCTION

In October of 1990, Mr. Richard Brezina of the Maryland Geological Society discovered an important fossil site east of Fredericksburg, in eastern Stafford County, Virginia (Fig. 1.1). This locality, along an unnamed tributary of Muddy Creek, became known as the Fisher/Sullivan site in recognition of its principle landowners. Mr. Brezina immediately realized that the site was exceptional, because it yielded numerous shark teeth and other vertebrate remains from the sands and gravels in the unnamed tributary. Mr. Brezina notified other members of the Maryland Geological Society, and together members of the MGS began to screen stream sediments at the site for more shark teeth and other remains. It soon became apparent, from the types of teeth that were being found and from the color and texture of the sediments in the banks of the creek, that the fossils were being reworked from glauconitic ("greensand") horizons of the Lower Tertiary (Paleocene-Eocene) Pamunkey Group (Fig. 1.2). Because the Pamunkey Group previously had yielded only sparse vertebrate remains, it seemed reasonable to suspect that this locality was scientifically important.

Consequently, an assessment of the potential scientific value of the site was begun. As part of this process, a stratigraphic column was compiled of the sequence of sediments exposed in the stream banks. The column was found to be nearly barren of vertebrate fossils, except for a two foot-thick layer that contained abundant teeth and bones. This layer clearly was the source of the teeth and bones being found in the stream bed sands and gravels. Once the source bed for the fossils was located, several members of the Maryland Geological Society approached the landowners, Mr. Rick DeBernard, Mr. Dennis Fisher, Mr. Larry Fisher, and Mr. Russell Sullivan, to see if they would allow the MGS to conduct systematic excavations directly into the fossiliferous layer. Fortunately, all of the land owners were public-minded and granted permission to allow the project to proceed. Subsequently, over a period of several years, members of the MGS excavated tons of sediment from the fossiliferous layer and washed them through screens to extract their fossil content. The work was long, arduous, and tedious, but eventually the MGS amassed an impressive quantity and variety of fossil vertebrate specimens, as well as a number of fossil fruits and nuts.

The sheer abundance and diversity of the material from the Fisher/Sullivan site made it impossible for any single individual to adequately describe and evaluate all of it. Therefore, subsets of the fossil material were made available by MGS club members to a number of interested professional scientists. These researchers were able to compile a large body of scientifically important information about the collections. This information obviously would be most useful if it could be published together, so the Maryland Geological Society contacted the Virginia Division of Mineral Resources to see if VDMR would be willing to publish the findings of this detailed and diverse research effort. VDMR graciously agreed to do so, and the present volume is the result.

Although the Fisher/Sullivan site has produced by far the best sample of early Eocene vertebrates and land plants so far found in Virginia or Maryland, it must be understood that the story still is far from complete. More than one hundred species of vertebrates now are known from this one horizon, but even so, many more species probably remain to be discovered. Marine vertebrates are disproportionately represented, because the depositional environment of the Fisher/Sullivan site was shallow marine. Although sharks and rays are well represented (see Kent, Parts 2 and 3 of this volume), the fossil marine bony fishes found to date account for less than half of the total number of species that probably then existed (see Weems, Part 4 of this volume). Vertebrates and plants that lived nearby on land and in rivers are even more poorly represented, because their remains had to wash out to sea to be preserved (see Weems, Part 5; Olson, Part 6; Rose, Part 7; and Tiffney, Part 8 of this volume). It can be surmised, from the number of species of vertebrates and plants found elsewhere at early Eocene terrestrial fossil localities, that only a tiny fraction of the total number of terrestrial species then present in Virginia have been sampled.

Even so, the present volume represents a major advance in our understanding of the Early Tertiary history of Virginia. From the single locality discussed here, nearly twice as many vertebrate and plant species have been recognized as have been described previously from all known sites within the Pamunkey Group throughout Maryland and Virginia (Clark and Martin, 1901; Gildersleeve, 1933; Lynn, 1934; Blake, 1940, 1941; Leriche, 1942; Weems and Horman, 1983; Tiffney, 1984; Weems, 1984, 1988; Case, 1989; Ward and Weist, 1990; Kent, 1994; Olson, 1994). Thanks to a unique and remarkable display of cooperation among land owners, amateur collectors, professional paleontologists, and the

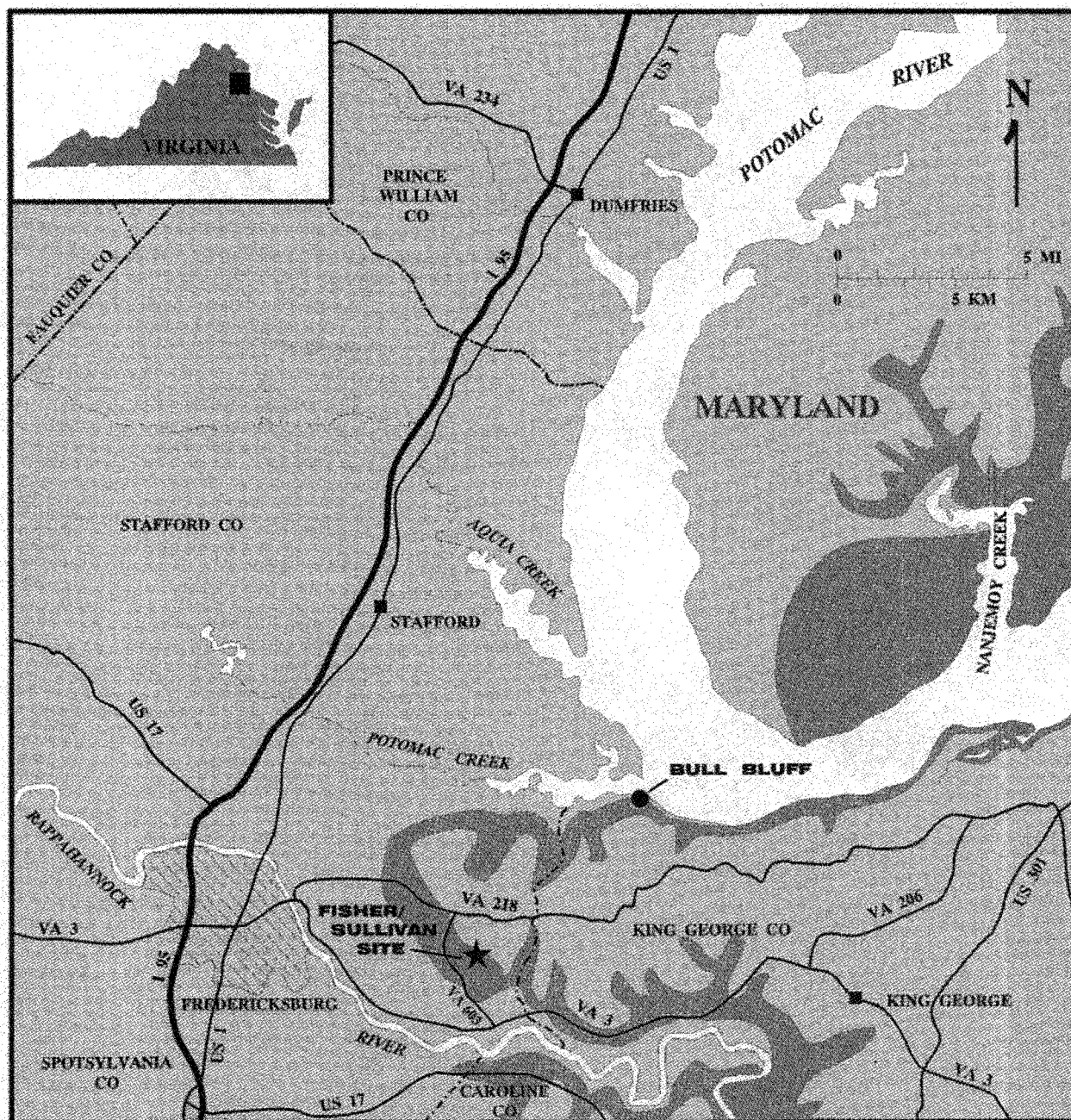


Figure 1.1. Map showing the general location of the Fisher/Sullivan site (star) in relationship to surrounding areas. Bull Bluff (solid circle), which contains a similar stratigraphic section, is shown to the northeast of the Fisher/Sullivan site. Outcrop belt of the lower Eocene Nanjemoy Formation is shown in dark gray. Area to the west of the Nanjemoy outcrop belt is underlain by older (underlying) sediments and rocks; area to the east is underlain by younger (overlying) Tertiary sediments. Surficial Quaternary deposits, which occur locally throughout the map area, are not shown. North of the Potomac River, the Nanjemoy strikes northeast, while south of the Potomac the strike shifts toward the south. The Nanjemoy dips gently to the east or southeast at about 15 feet per mile, an angle of less than 1 degree.

Virginia Division of Mineral Resources, this volume for the first time offers a rich and detailed picture of the life and environment that existed in Virginia during the early Eocene epoch. While still incomplete, this picture is orders of magnitude more detailed than anything that could have been imagined even five years ago.

### GEOLOGIC SETTING

The Fisher/Sullivan site is located within the outcrop belt of the Pamunkey Group, a sequence of Lower Tertiary (Paleocene-Eocene) sands and clays that formed in shallow marine environments beneath the western margin of the Atlantic Ocean. From bottom to top, the Pamunkey Group

includes the Paleocene Brightseat and Aquia Formations, the Marlboro Clay, and the Eocene Nanjemoy and Piney Point Formations (Figure 1.2). Downstream and stratigraphically beneath the Fisher/Sullivan site, an eight foot-thick section of the distinctive Marlboro Clay is exposed (see table 1 and Figure 1.3). Therefore the Fisher/Sullivan site, which lies stratigraphically about fifteen feet above the top of this Marlboro Clay outcrop, is within the lower part of the Nanjemoy Formation.

In all respects but one, the stratigraphy of the Fisher/Sullivan site compares readily to the stratigraphy established by Clark and Martin (1901) for the Nanjemoy Formation at Bull Bluff on the Potomac River about six miles to the northeast (Figure 1.1). In most outcrops other than Bull Bluff, the clayey sands at the top of the Aquia Formation (Figure 1.2) grade rapidly upward into the Marlboro Clay (Clark and Martin, 1901; Clark and Miller, 1912). The Marlboro Clay in turn is capped by a regional unconformity that separates it from the overlying Nanjemoy Formation (Glaser, 1971). The exposed section at Bull Bluff is atypical, in that the erosional unconformity at the base of the Nanjemoy has cut deeply enough into the underlying sediments to remove nearly all of the Marlboro Clay. As a result, the Nanjemoy rests directly upon the top of the Aquia Formation at Bull Bluff (Figure 1.3), except in a few local areas where thin remnants of the basal Marlboro Clay have been preserved (Thomas Gibson, personal communication).

Above this unconformity, Clark and Martin (1901) defined a sequence of beds in the Nanjemoy Formation that they called "zones" 10 through 17 (Figure 1.3). "Zone" 10 is a greensand (glauconitic sand), coarse at its base but fining upward, that is largely devoid of fossils. It is overlain by a thin bed of poorly sorted fine- to coarse-grained calcareous greensand ("zone" 11) that contains numerous shells, bones, and teeth. Above this, "zone" 12 is a fine-grained greensand that contains more or less continuous shell bands full of the bivalve mollusk *Venericardia potapacoensis*.

At the Fisher/Sullivan site, in contrast to the deeply channeled section exposed at Bull Bluff, the Marlboro Clay is present and well developed (Figure 1.3). As is regionally typical, the top of the Marlboro Clay is deeply and prominently burrowed and overlain by a thin deposit of sparsely fossiliferous medium- to coarse-grained greensand that grades upward into a much finer green-sand (Table 1). This layer of largely unfossiliferous greensand extends upward to the base of the bone-bearing bed at the Fisher/Sullivan site. The bone-bearing bed constitutes a second relatively coarse greensand layer within the Nanjemoy Formation that in turn grades upward into a second much finer greensand. However, unlike the greensand bed beneath the bone-bearing horizon, the greensand bed above the bone-producing horizon contains thin, more or less continuous shell bands full of the bivalve mollusk *Venericardia potapacoensis*.

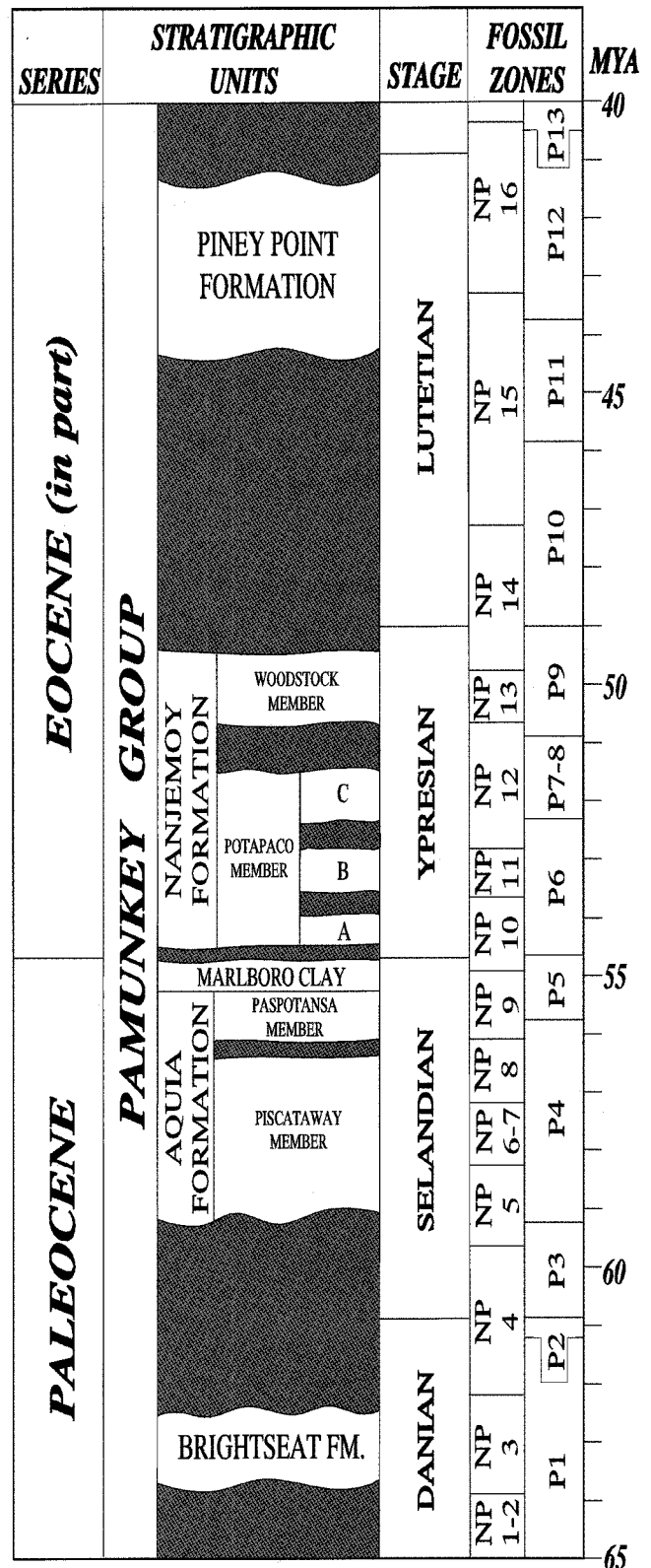


Figure 1.2. Stratigraphic section of the Pamunkey Group, showing the age and sequence of its constituent formations, members, and beds. The Fisher/Sullivan site is located at the base of bed B of the Potapaco Member of the Nanjemoy Formation. Time intervals missing at unconformities are indicated by dark-gray shading. Fossil zones and ages after Berggren and others (1995).

Locally, small pockets of teeth and bones have been found up to a foot or two beneath the main bone-bearing bed. It appears likely that these represent infillings of burrows that were dug into the underlying unit by marine organisms at the time the bone bed was accumulating.

Except for the presence of a considerable thickness of the Marlboro Clay, the section exposed at the Fisher/Sullivan

site is nearly identical to the section exposed at Bull Bluff (Figure 1.3). Notably, the combined thickness of Clark and Martin's "zone" 10 and the Marlboro Clay at the Fisher/Sullivan site is nearly identical to the total thickness of "zone" 10 at Bull Bluff, where the Marlboro Clay mostly has been cut out of the local section and replaced by an unusually thick layer of "zone" 10 greensand. In all respects except

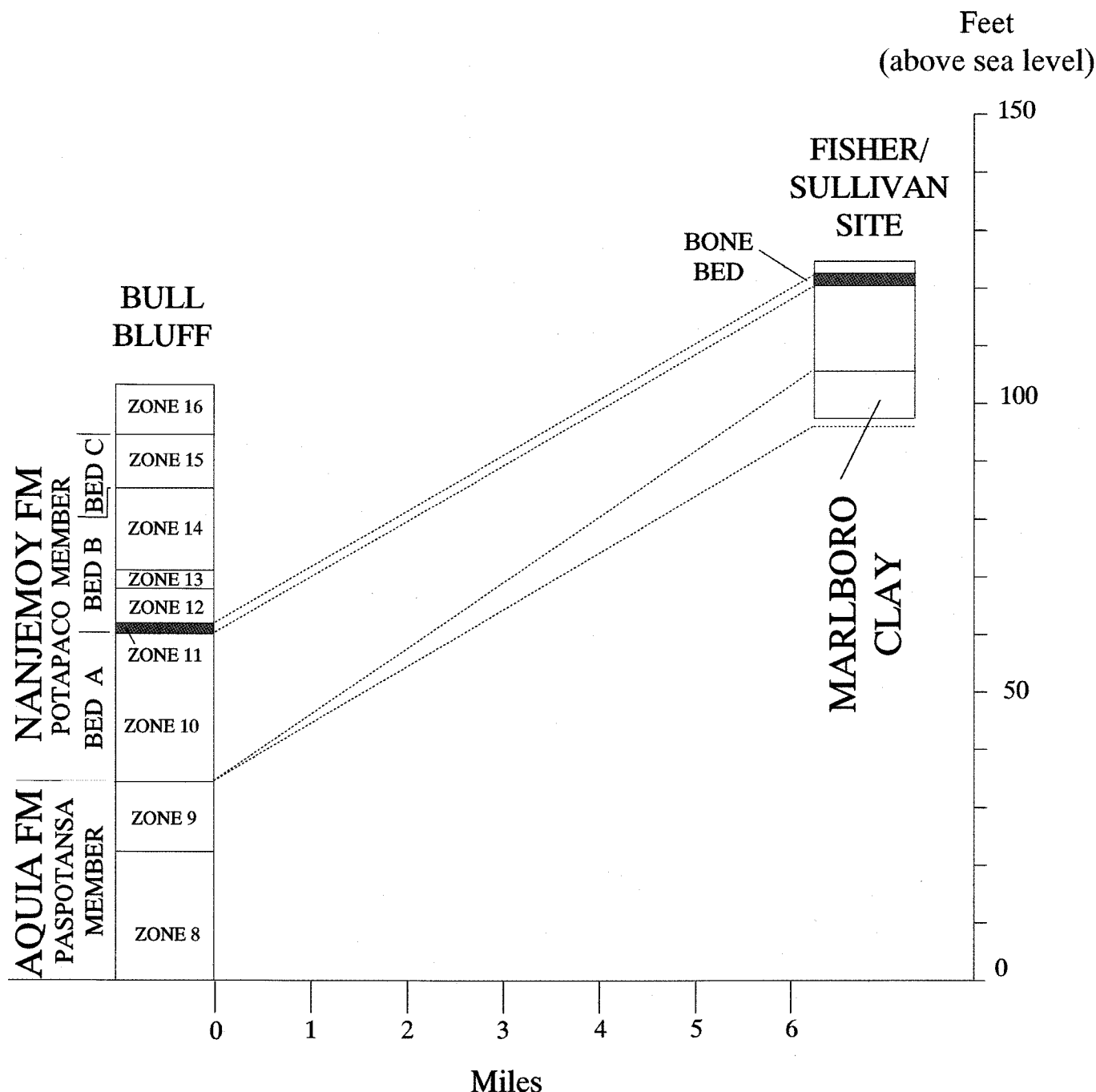


Figure 1.3. Comparison of the stratigraphic section exposed at the Fisher/Sullivan site with the stratigraphic section exposed at Bull Bluff on the Potomac River located 6 miles to the northeast. Bull Bluff is the standard reference section for the lower portion of the Nanjemoy Formation. Bull Bluff section adapted from Clark and Martin (1901), Fisher/Sullivan site section compiled by Gary J. Grimsley and Robert E. Weems.

Table 1. Geologic section exposed at the Fisher/Sullivan site, Stafford County, Virginia

Unit	Bed	Description	Thickness (feet)
<b>Nanjemoy Formation</b>  (Potapaco Member)	B	Sand, dominantly quartz, fine-grained, well sorted, micaceous, glauconitic, medium-brown, sparse wood fragments present and molds and casts of shells.....	1
	B	Sand, dominantly quartz, dominantly fine-grained but with abundant rounded grains of medium- to coarse-grained quartz and scattered rounded quartz granules and pebbles to 1 cm in diameter, glauconitic, medium-brown, contains abundant shell casts of <i>Venericardia potapacoensis</i> and abundant teeth and bones.....	2
	------(Unconformity)-----		
	A	Sand, dominantly quartz, very fine- to fine-grained, bioturbated and massive, glauconitic, medium-brownish-gray, scattered wood fragments throughout and scattered molds and casts of shells, upper foot bioturbated and burrows filled with matrix from above bed, basal foot contains abundant medium- to coarse-grains and is more glauconitic than sediments above.....	15
	------(Unconformity)-----		
<b>Marlboro Clay</b>		Clay, silty, finely micaceous, greasy, sticky, light-gray, upper two feet intensely burrowed and burrows filled with matrix from bed above.....	8
Total section exposed.....			26

total thickness, the interval beneath the bone-bearing layer at the Fisher/Sullivan site is identical to the layer called "zone" 10 by Clark and Martin (1901). The bone-bearing interval similarly is identical to the layer called "zone" 11 by Clark and Martin (1901), and the overlying bed is identical to the lower part of their "zone" 12. Therefore, the stratigraphy at the Fisher/Sullivan site can be matched confidently to the Nanjemoy "zones" defined by Clark and Martin at Bull Bluff. In recent years, Clark and Martin's "zones" have been superseded by a new zonation for the lower Nanjemoy. In this newer classification (Ward, 1985), Clark and Martin's "zone 10" is renamed "Potapaco Bed A",

while "zones" 11 and 12 are the lower part of "Potapaco Bed B". The upper part of Potapaco Bed B is not exposed at the Fisher/Sullivan locality.

Biostratigraphic studies of Early Tertiary outcrops exposed in the Potomac River valley (Gibson and Bybell, 1991), as well as studies of nearby cores (Reinhardt and others, 1980; Gibson and others, 1980; Mixon and others, 1989), have established an accurate stratigraphic framework for the Pamunkey Group column. It is now known that the unconformity that lies between the basal Potapaco Member of the Nanjemoy Formation and the Marlboro Clay (Figure 1.2) appears to include the Paleocene-Eocene boundary (Gibson and Bybell, 1991; Frederiksen, 1979). Potapaco Bed A (= "zone" 10 of Clark and Martin, 1901) can be assigned to calcareous nannofossil zone NP10 (Gibson and Bybell, 1991), which is very early Eocene in age. This bed is separated from the overlying early Eocene Potapaco Bed B by another unconformity. Above this second unconformity lies the basal lag bed of Potapaco Bed B (= "zone" 11 of Clark and Martin, 1901), which at the Fisher/Sullivan site also includes abundant bones and teeth. Potapaco Bed B has been assigned to calcareous nannofossil zone NP11 (Gibson and Bybell, 1991). The best estimate for the age of zone NP11 encompasses the time interval of 53.6 to 52.8 million years ago (Berggren and others, 1995). This time interval also corresponds to the middle of the Wasatchian North American land mammal "age" of the western United States (Prothero, 1995).

These stratigraphic relationships are summarized in Figure 1.2, and the Pamunkey Group units also are shown in relationship to the best available estimates for the age of the Lower Tertiary section found in southeastern England (Figure 1.4). The English section appears to overlap broadly in age with the Pamunkey Group section, and this conclusion is strongly supported by the occurrence of many fossil species at the Fisher/Sullivan site that were originally described from the English Lower Tertiary (see subsequent sections of this volume).

Despite intensive collecting over the last several years, the only other part of the Fisher/Sullivan section that has yielded even a few fish teeth and seeds is the basal "Potapaco A" ("zone" 10) lag bed of the Nanjemoy, which lies below the main bone bed ("zone" 11). No other horizons exposed at this site have produced any fossil vertebrate remains. This implies that the material from the main bone-bed at the Fisher/Sullivan site represents an exceptionally uncontaminated sample of a very narrow time-horizon within the Coastal Plain section. There are other horizons in other marine stratigraphic units of the Coastal Plain that produce vertebrate remains in some abundance. In most of these other cases, as at the Fisher/Sullivan site, they occur in the basal foot of units that contain only sparse vertebrate remains throughout the rest of their columns. In these other occurrences, however, the basal foot of sediment usually contains large quantities of detrital lag material of diverse ages that was present on the sea floor at the time that

NP	P			HAMPSHIRE AND ISLE OF WIGHT	THAMES VALLEY AND ESTUARY	VIRGINIA AND MARYLAND	
17	14	EOCENE (in part)	MIDDLE	BRACKELSHAM GROUP	BARTON BEDS	PINEY POINT FORMATION	
	13						
16	12						
15	11						
14	10						
13	9	EOCENE (in part)	EARLY	BRACKELSHAM GROUP	BAGSHOT FORMATION	WOODSTOCK MEMBER	
	8						
12	7						
11	6						
10							
9	5	PALEOCENE (in part)	LATE	READING FORMATION	READING/WOOLWICH BEDS	MARLBORO CLAY	
8	4						
7							
6							
5	3					PISCATAWAY MEMBER	

Figure 1.4. Comparison of the Pamunkey Group section with the stratigraphic section exposed in the London basin (southeast England). London section adapted from Curry and others (1978). The strata in the two basins broadly overlap in age.

deposition of the unit began. Typically, this detrital material includes significant quantities of vertebrate and other fossil remains that were reworked into the overlying bed from one or more underlying beds of much greater age. At the Fisher/Sullivan site, however, there is nothing to indicate that the underlying bed ever contained vertebrate material that could have been reworked. Moreover, even if there is any undetected reworked material, it still came from a local bed only slightly older in age. This conclusion is in accord with the excellent preservation of most of the fossil material described here, which could not have been transported very far. While it is true that most of the fossil remains seem to have come from carcasses that were disarticulated and slightly scattered before burial, individual bones are too fresh and unworn to have suffered from prolonged scavenging or transport.

The preceding observations strongly indicate that the fauna and flora recovered from the Fisher/Sullivan site represent a sample of life from within a very narrow time

segment of the early Eocene, most probably confined to only the early part of calcareous nannoplankton Zone NP11. Because the Fisher/Sullivan sample represents only a small segment of time, the fauna and flora are exceptionally useful for estimating the diversity of life that was present, determining the climate that then existed, establishing the local depositional environment, and correlating this horizon with other vertebrate and plant producing beds in North America, Europe, and elsewhere.

#### PALEOGEOGRAPHIC SETTING

About 53 million years ago, when the Fisher/Sullivan fauna and flora were being entombed, Earth processes already had established the geologic framework of the region that later would be called Virginia. The mid-Atlantic Ridge spreading center, when it formed about 175 million years ago, broke apart the supercontinent of Pangaea and initiated the opening and expansion of the modern Atlantic

Ocean basin (Manspeizer, 1988). With the initiation of this rifting event, North America became separated from Africa and the area that today constitutes the state of Virginia became part of the trailing edge of the newly-formed North American continent.

After rifting and sea floor spreading had created the Atlantic Ocean basin, the eastern margin of the future state of Virginia began to subside and accumulate sediment beneath the edge of the early Atlantic Ocean. This accumulating wedge of sediment, thin in the west but thousands of feet thick in the east, ultimately became both the Coastal Plain of Virginia and the floor of the Atlantic Ocean coastal marine shelf of the present day state. Although the one area today is above the ocean and the other below it, from a geologic perspective the two areas are continuous and underlain by similar sediments.

Even though the Coastal Plain of today existed as a geologic feature in the early Eocene, it would not have been readily recognizable to a time traveler visiting that distant age. This is because, in early Eocene time, nearly all of the modern Coastal Plain of Virginia was submerged beneath the Atlantic Ocean, and the shoreline probably was at or near the present Fall Line (roughly marked today by Interstate Highway 95). Sediment accumulating beneath this sea eventually would compact to become the Nanjemoy Formation millions of years later.

The layers of marine sediment accumulating across the Atlantic Coastal Plain during early Eocene time were relatively thin and well sorted. For the most part, these sediments also were much more mature mineralogically than the sediments that are being transported today along the modern riverways of Virginia. These sorting and mineralogical characteristics of the early Eocene sediments indicate that their source areas, the modern Piedmont Province, Blue Ridge, and Appalachian regions of Virginia, then were deeply weathered and were contributing a much smaller volume of sediment to the coastal region than they do today (Gibson, 1970; McCartan, 1989). This in turn implies that, during early Eocene time, flat to gently rolling landforms probably existed across all the central and western part of the state. If any mountains existed at all, they were only isolated inselbergs similar to Willis Mountain in Buckingham County, or Sugarloaf Mountain in Maryland, standing in isolation far from any other scattered peaks that might have persisted from a much earlier time of more mountainous relief.

In addition to striking differences in the topography and geography of Virginia, as compared to modern times, a time traveler to the early Eocene also would find the global position of Virginia very strange (Fig. 1.5). Since the Atlantic Ocean began to form in the Middle Jurassic Period, about 175 million years ago, it has widened steadily to its present size. Although the Atlantic Ocean was large by the early Eocene, it still was considerably narrower than it is today. This was particularly noticeable in two areas. In the northern part of the North Atlantic Ocean basin, Greenland

and Britain were close together and Iceland did not yet exist. Similarly, the distance between South America and Africa also was much shorter. If the South Atlantic and the North Atlantic had been given names in those days, they probably would have been named as separate oceans.

The smaller size of the Atlantic Ocean, as compared to today, made migration back and forth across it relatively simple for marine animals and plants. This ease of interchange is strikingly reflected in the faunal reports on marine vertebrates that follow, for most of these taxa are found as fossils on both sides of the modern Atlantic. Similarly, some researchers have come to believe that a land-bridge existed during early Eocene time that directly connected western Europe with eastern North America by way of Greenland. This land bridge has been hypothesized because closely related terrestrial plants and animals have been found on both sides of the North Atlantic. Somehow, they or their immediate ancestors must have crossed between Europe and North America (McKenna, 1983; Tiffney, 1985; Frederiksen, 1994). The birds (Olson, Part 6 of this volume) and plants (Tiffney, Part 8 of this volume) from the Fisher/Sullivan site readily seem to support this hypothesis. The mammals from the Fisher/Sullivan site, however, so far show a stronger affinity to western North America than to Europe (Rose, Part 7 of this volume). These observations (so far including only a very few taxa of mammals) may suggest either that early Eocene migration between Europe and North America was easier for birds and plants than for mammals, or else that the land bridge connection had been broken just prior to the time interval represented at the Fisher/Sullivan site. The latter interpretation would be consistent with a recent estimate (Tegner and others, 1998) that rifting of East Greenland from western Europe occurred between 57 and 54 million years ago, just prior to the time (about 53 million years ago) represented by the Fisher/Sullivan site.

Another striking contrast between the modern world and the early Eocene world is that the area we now call Virginia then was much warmer. The flora that has been recovered (Tiffney, 1984, Part 8 of this volume; Frederiksen, 1994), the marine vertebrates (Kent, Parts 2 and 3 of this volume; Weems, Part 4 of this volume), the reptiles (Weems, Part 5 of this volume), and the birds (Olson, Part 6 of this volume) all indicate an environment that was much warmer, wetter, more equable, and more tropical than the strongly seasonal and temperate environment that exists today. This accords well with a large body of data, collected from around the world, that indicates the Earth experienced its warmest interval of the past 65 million years during the early Eocene (e.g., Frakes, 1979; Shackleton and Boersma, 1981; Wolfe, 1985; Barron, 1987; Crowley and North, 1991; Markwick, 1994; Sloan, 1994; Sloan and Rea, 1995). At that time, warm and equable conditions spread as far north as the Arctic region, where remains of alligators and turtles have been found even on Ellesmere Island in the Canadian Arctic (Estes and Hutchison, 1980). In the deep oceans, tempera-

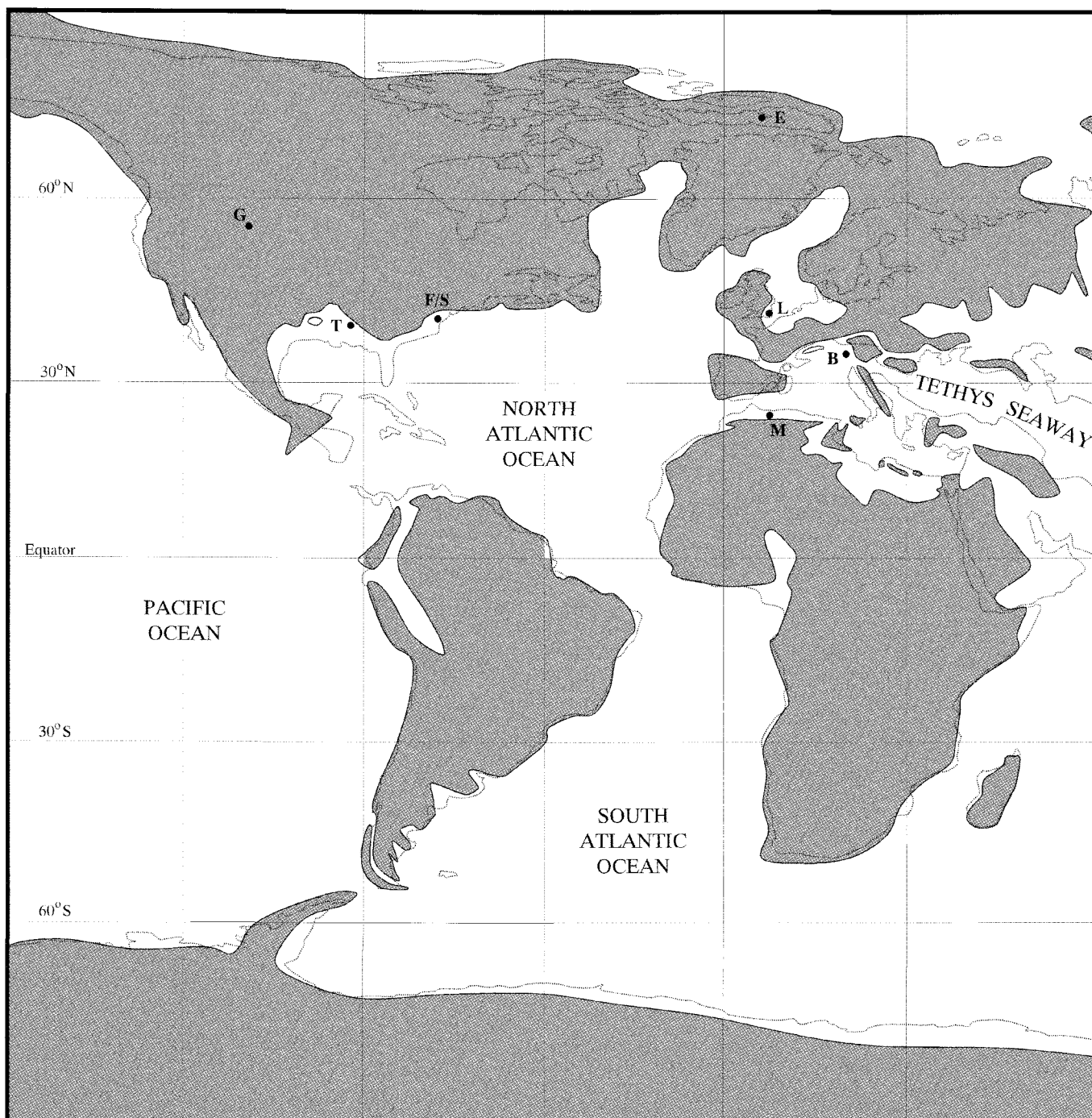


Figure 1.5. Paleogeographic map of the Atlantic basin and surrounding continents in the early Eocene, about 50-55 million years ago (adapted from Smith and others, 1994). The location of the Fisher/Sullivan site in Virginia (F/S) is indicated, as well as the location of the Green River beds in Utah and Wyoming (G), the Tuscahoma Formation in Mississippi (T), the Ellesmere Island fauna in the Canadian Arctic (E), the London basin in England (L), Monte Bolca in Italy (B), and the Moroccan phosphate horizons (M). Many of the taxa of fossil vertebrates described in this volume were first described from these areas. Note that the Atlantic basin was much narrower in the early Eocene than it is today, and that a land bridge probably existed across Greenland between western Europe and northeastern North America.

ture studies indicate that the water there also was much warmer than today (Douglas and Woodruff, 1981). Thus, it is not too surprising that several of the papers in the present volume suggest that the early Eocene climate of Virginia probably was as warm as central or southern Florida today.

Even though the early Eocene topography and climate of Virginia might have seemed reminiscent of southern Florida, the animals and plants that inhabited that landscape would have quickly belied the similarities. As the following articles on reptiles, birds, mammals, and land plants show, many of the early Eocene land-dwelling plants and animals in Virginia were far different from those living in North America today, and many have their closest affinities with animals and plants now living in southeast Asia. Curiously, this radical difference in the land life is not mirrored closely by the fish fauna from the marine realm. As the following articles on sharks, rays, and bony fishes show, the marine fish fauna was strikingly similar to that found off the east coast of Florida today. This implies that marine fishes have not suffered nearly so much stress and change as have the inhabitants of the land environment, even though the marine environment certainly has cooled markedly during subsequent geologic time.

## BIBLIOGRAPHY

- Barron, E.J., 1987, Eocene equator-to-pole surface ocean temperatures; a significant climate problem?: *Paleoceanography* 2:729-739.
- Berggren, W.A., Kent, D.V., Swisher, C.C., III, and Aubry, M.-P., 1995, A revised Cenozoic geochronology and chronostratigraphy: Society of Economic Paleontologists and Mineralogists Special Publication 54, p. 129-212.
- Blake, S.F., 1940, *Paralbula*, a new fossil fish based on dental plates from the Eocene and Miocene of Maryland: Washington Academy of Sciences Journal 30:205-209.
- Blake, S.F., 1941, Note on a vertebra of *Palaeophis* from the Eocene of Maryland: Washington Academy of Sciences Journal 31:501-503.
- Case, G.R., 1989, *Palaeocarcharodon orientalis* (Sinuow) (Neoselachii: Cretoichthyidae) from the Paleocene of Maryland, USA: *Palaeovertebrata* 19(1):1-6.
- Clark, W.B., and Martin, G.C., 1901, The Eocene deposits of Maryland: Maryland Geological Survey, Eocene Volume, 331 pp.
- Clark, W.B., and Miller, B.L., 1912, Physiography and geology of the Coastal Plain province of Virginia: Virginia Geological Survey Bulletin 4:1-274.
- Crowley, T.J., and North, G.R., 1991, *Paleoclimatology*: New York, Oxford University Press, 339 pp.
- Curry, D., Adams, C.G., Boulter, M.C., and others, 1978, A correlation of Tertiary rocks in the British Isles: Geological Society of London, Special Report 12:1-72.
- Douglas, R.G., and Woodruff, Faye, 1981, Deep sea benthic foraminifera, in C. Emiliani, ed., *The Sea* (New York, Wiley Interscience) 7:1233-1327.
- Estes, Richard, and Hutchison, J.H., 1980, Eocene lower vertebrates from Ellesmere Island, Canadian Arctic Archipelago: *Palaeogeography, Palaeoclimatology, Palaeoecology* 30:325-347.
- Frakes, L.A., 1979, *Climates through geologic time*: Amsterdam, Elsevier, 310 pp.
- Frederiksen, N.O., 1979, Sporomorph biostratigraphy, northeastern Virginia: *Palynology* 3:129-167.
- Frederiksen, N.O., 1994, Paleocene floral diversities and turnover events in eastern North America and their relation to diversity models: Review of *Palaeobotany and Palynology* 82:225-238.
- Gibson, T.G., 1970, Late Mesozoic-Cenozoic tectonic aspects of the Atlantic Coastal margin: Geological Society of America Bulletin 81:1813-1822.
- Gibson, T.G., Andrews, G.W., Bybell, L.M., Frederiksen, N.O., Hansen, Thor, Hazel, J.E., McLean, D.M., Witmer, R.J., and van Nieuwenhuise, D.S., 1980, Biostratigraphy of the Tertiary strata of the core: in *Geology of the Oak Grove core, Virginia Division of Mineral Resources Publication* 20, p. 14-40.
- Gibson, T.G., and Bybell, L.M., 1991, Paleocene-Eocene boundary sedimentation in the Potomac River Valley, Virginia and Maryland: IGCP Project 308, Fieldtrip Guidebook, 124 pp.
- Gildersleeve, Benjamin, 1933, Pharyngeal plates of *Phyllodus* from the Virginia Eocene: Washington Academy of Science Journal 23:380-389.
- Glaser, J.D., 1971, Geology and mineral resources of southern Maryland: Maryland Geological Survey Report of Investigations 15:1-84.
- Kent, B.W., 1994, Fossil sharks of the Chesapeake Bay region: Columbia, Maryland, Egan Rees and Boyer, Inc., 146 p.
- Leriche, Maurice, 1942, Contribution à l'étude des faunes ichthyologiques marines des terrains tertiaires de la Plaine Cotière Atlantique et du centre des États-Unis: Mémoires de la Société Géologique de France (n.s.) 20(45): 1-111.
- Lynn, W.G., 1934, A new snake (*Paleophis virginianus*) from the Eocene of Virginia: Johns Hopkins University Studies in Geology 11:245-249.
- Manspeizer, Warren, 1988, Triassic-Jurassic rifting and opening of the Atlantic; an overview: in Manspeizer, Warren, ed., *Triassic-Jurassic rifting; Continental breakup and the origin of the Atlantic Ocean and passive margins*: (New York, Elsevier) *Developments in Geotectonics*, volume 22, part A, p. 41-79.
- Markwick, P.J., 1994, "Equability," continentality, and Tertiary "climate": the crocodilian perspective: *Geology* 22:613-616.
- McCartan, Lucy, 1989, Mineralogy of the Haynesville, Virginia cores: in Mixon, R.B., ed., *Geology and paleontology of the Haynesville cores -- northeastern Virginia Coastal Plain*: United States Geological Survey Professional Paper 1489, p. B1-B9.

- McKenna, M.C., 1983, Cenozoic paleogeography of North Atlantic land bridges: *in* M.H.P. Bott, S. Saxov, M. Talwani, and J. Thiede (editors), *Structure and development of the Greenland-Scotland Ridge*: New York, Plenum, p. 351-399.
- Mixon, R.B., Powars, D.S., Ward, L.W., and Andrews, G.W., 1989, Lithostratigraphy and molluscan and diatom biostratigraphy of the Haynesville cores -- outer Coastal Plain of Virginia: *in* Mixon, R.B., ed., *Geology and paleontology of the Haynesville cores -- northeastern Virginia Coastal Plain*: United States Geological Survey Professional Paper 1489, p. A1-A48.
- Olson, S.L., 1994, A giant *Presbyornis* (Aves: Anseriformes) and other birds from the Paleocene Aquia Formation of Maryland and Virginia: *Proceedings of the Biological Society of Washington* 107(3):429-435.
- Prothero, D.R., 1995, Geochronology and magnetostratigraphy of Paleogene North American land mammal "ages": an update: *Society of Economic Paleontologists and Mineralogists Special Publication* 54, p. 305-315.
- Reinhardt, Juergen, Newell, W.L., and Mixon, R.B., 1980, Tertiary lithostratigraphy of the Core: *in* *Geology of the Oak Grove core*: Virginia Division of Mineral Resources Publication 20, p. 1-13.
- Shackleton, N.J., and Boersma, A., 1981, The climate of the Eocene ocean: *Journal of the Geological Society of London* 138:153-157.
- Sloan, L.C., 1994, Equable climates during the early Eocene: Significance of regional paleogeography for North American climate: *Geology* 22:881-884.
- Sloan, L.C., and Rea, D.K., 1995, Atmospheric carbon dioxide and early Eocene climate: A general circulation modeling sensitivity study: *Palaeogeography, Palaeoclimatology, Palaeoecology* 119(3-4):275-292.
- Smith, A.G., Smith, D.G., and Funnell, B.M., 1994, *Atlas of Mesozoic and Cenozoic coastlines*: New York, Cambridge University Press, 99 pp., 31 maps.
- Tegner, C., Duncan, R.A., Bernstein, S., Brooks, C.K., Bird, D.K., and Storey, M., 1998,  $^{40}\text{Ar}$ - $^{39}\text{Ar}$  geochronology of Tertiary mafic intrusions along the East Greenland rifted margin: Relation to flood basalts and the Iceland hotspot track: *Earth and Planetary Science Letters*, 156(1-2):75-88.
- Tiffney, B.H., 1984, Fossil fruits from the Woodstock Member of the Nanjemoy Formation, Maryland and Virginia: *in* Ward, L.W., and Krafft, Kathleen, eds., *Stratigraphy and paleontology of the outcropping Tertiary beds in the Pamunkey River region, central Virginia Coastal Plain*, Guidebook for the Atlantic Coastal Plain Geological Association 1984 field trip, Atlantic Coastal Plain Geological Association, p. 150-154.
- Tiffney, B.H., 1985, The Eocene North Atlantic land bridge: its importance in Tertiary and modern phytogeography of the northern hemisphere: *Journal of the Arnold Arboretum* 66(2):243-273.
- Ward, D.J., and Weist, R.L., Jr., 1990, A checklist of Paleocene and Eocene sharks and rays (Chondrichthyes) from the Pamunkey Group, Maryland and Virginia, U.S.A.: *Tertiary Research* 12(2):81-88.
- Ward, L.W., 1985, Stratigraphy and characteristic mollusks of the Pamunkey Group (lower Tertiary) and the Old Church Formation of the Chesapeake Group -- Virginia Coastal Plain: United States Geological Survey Professional Paper 1346, 78 pp.
- Weems, R.E., 1984, Vertebrate biozones of the Pamunkey Group (Paleocene and Eocene, Maryland and Virginia): *in* Ward, L.W., and Krafft, Kathleen, eds., *Stratigraphy and paleontology of the outcropping Tertiary beds in the Pamunkey River region, central Virginia Coastal Plain*, Guidebook for the Atlantic Coastal Plain Geological Association 1984 field trip, Atlantic Coastal Plain Geological Association, p. 198-204.
- Weems, R.E., 1988, Paleocene turtles from the Aquia and Brightseat Formations, with a discussion of their bearing on sea turtle evolution and phylogeny: *Proceedings of the Biological Society of Washington* 101:109-145.
- Weems, R.E., and Horman, S.R., 1983, Teleost fish remains (Osteoglossidae, Blochiidae, Scombridae, Triodontidae, Diodontidae) from the Lower Eocene Nanjemoy Formation of Maryland: *Proceedings of the Biological Society of Washington* 96(1):38-49.
- Wolfe, J.A., 1985, Distribution of major vegetational types during the Tertiary: *in* Sundquist, E.T., and Broecker, W.S., eds., *The Carbon cycle and atmospheric CO<sub>2</sub>, natural variations, Archean to present*: Washington, DC, American Geophysical Union Geophysical Monograph 32:357-375.

## PART 2. SHARKS FROM THE FISHER/SULLIVAN SITE

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### INTRODUCTION

Sharks have a long, rich fossil record, due in large part to the regular, and continual, replacement of teeth during life (Maisey, 1984). This abundance of teeth means that sharks have, in one sense, the best fossil record of any vertebrate, and in another sense, the worst. In most Mesozoic and Cenozoic marine fossil beds, shark teeth are the most abundant vertebrate fossils, providing an enormous number of specimens for study and analysis. But in these same beds, there are few of the other skeletal elements that would provide important additional information for understanding the evolution of sharks. Consequently, reconstructions of evolutionary relationships among fossil sharks are strongly influenced by changes in tooth morphology, and constitute little more than studies in dental evolution. Such studies, although biased by the nature of the available fossils, are nonetheless extremely helpful, since teeth contain a wealth of useful information. Further, teeth appear to be particularly valuable for tracing lineages over a range of time scales, since crown morphology is evolutionarily plastic (i.e., changes rapidly during speciation), while root structure is evolutionarily stable (i.e., is conserved over comparatively long periods of time; Kent, 1994; unpublished data).

The Fisher/Sullivan Bone Bed contains a highly diverse assemblage of fossil shark species. A total of thirty-two fossil shark species (in seven orders and sixteen families) have been recorded from this relatively restricted horizon. Due to the absence of reworked material from other fossiliferous horizons at this site (Weems and Grimsley, this volume), the Fisher/Sullivan Bone Bed provides a unique opportunity to examine a relatively intact and uncontaminated fossil shark community.

**Class Chondrichthyes Huxley, 1880**  
**Subclass Elasmobranchii Bonaparte, 1838**  
**Cohort Euselachii Hay, 1902**

**Order Hexanchiformes Buen, 1926**  
**Family Hexanchidae Gray 1851**

Hexanchid, or cow, sharks have six gill slits, a single, spineless dorsal fin located on the posterior half of the body and an elongated caudal fin (Figure 2.1). They have a cutting-grasping dentition, with grasping teeth in the upper jaw and distinctive multicusped cutting teeth in the lower jaw (Kent, 1994).

Cow sharks are primarily deepwater species that

infrequently venture into shallow, coastal waters. They are known to feed on a variety of foods, including, bony fishes, sharks, rays, crustaceans and carrion (Castro, 1983; Compagno, 1984). Cow sharks attain large sizes, with the extant *Hexanchus griseus* growing to at least 5.5 m (Clark and Kristof, 1990).

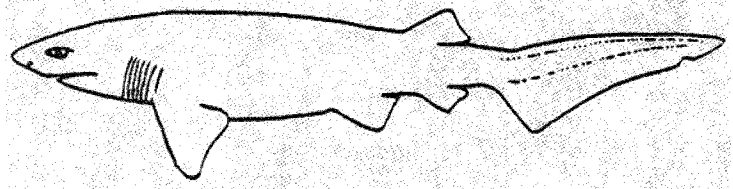


Figure 2.1. Cow shark.

**Genus *Hexanchus* Rafinesque 1810a**  
***Hexanchus* sp.**

**Figured Specimens:** Plate 2.1A-C.

**Description:** The lower antero-lateral teeth are multicusped, with up to ten robust cusps of graded sizes. The largest cusp is adjacent to the mesial margin of the tooth and has a serrated mesial edge. The remaining cusps become progressively smaller toward the distal tooth margin and are unserrated. The root is highly compressed, roughly rectangular, and wedge-shaped in cross-section. The mesial margin of the root is broadly and shallowly indented. Maximum tooth width is about 20 mm.

The upper antero-lateral teeth are narrower than the lower teeth, with proportionally fewer cusps. The first upper antero-lateral tooth usually has only a single cusp and a relatively robust root. More posterior upper antero-laterals exhibit an incremental increase in the number of cusps and a more pronounced compression of the root. The mesial edge of the root lacks the weak indentation found on lower antero-lateral teeth. The largest specimens have a width of about 11 mm.

Symphyseal teeth have a medial cusp with reduced cusps on either side. The exact form of the medial cusp is rather variable, ranging from large and erect to small and inclined to one side. The number of accessory cusps on each side of the medial cusp can vary from as few as two up to, at least, four. Symphyseal teeth are somewhat smaller than the previously discussed teeth in this species, with a maximum width of about 7 mm.

**Remarks:** As with other *Hexanchus*, there appears to be a

sexual dimorphism in lower antero-lateral tooth form (Kent, 1994). Female teeth have a primary cusp only slightly larger than the next cusp, while in male teeth the primary cusp is clearly larger than the second cusp.

*Hexanchus* sp. is a rare shark in the Fisher/Sullivan Bone Bed. The principally deepwater habitat of modern cow sharks is consistent with the rarity of this species in the relatively shallow water sediments of the Fisher/Sullivan Bone Bed.

There is some controversy as to the correct species designation of the *Hexanchus* teeth from the Fisher/Sullivan Bone Bed. Mike Hogan (personal communications) has made a careful study of numerous *Hexanchus* specimens, and believes those from the Fisher/Sullivan Bone Bed are morphologically closer to the Late Cretaceous species, *H. microdon*, than to the typical Eocene to Oligocene species, *H. agassizi*. The former species consistently has a relatively deeper root and more robust conules than the latter species. There is also some similarity between the Fisher/Sullivan specimens and *Hexanchus collinsonae* from the British Eocene (Ward, 1979). However, the markedly convex mesial cutting edges and tightly spaced conules usually seen in this species are not commonly found in Fisher/Sullivan Bone Bed specimens. The Fisher/Sullivan Bone Bed specimens most closely resemble the Early Eocene *Hexanchus* teeth illustrated in Arambourg (1952; as *Notidanus* sp.).

At present, the designation of the Fisher/Sullivan Bone Bed *Hexanchus* must remain unresolved. While most closely resembling Arambourg's Moroccan specimens, it is difficult to consistently separate the Moroccan species from *H. microdon* and *H. collinsonae*. Further study is needed to determine the correct species name for both the Fisher/Sullivan and Moroccan *Hexanchus*.

### Order Squaliformes Goodrich 1909a

Squaliform sharks are small, generally benthic, sharks with a cylindrical body, five gill slits, two dorsal fins and no anal fin. Although found in a variety of habitats, squaliforms are most abundant in deeper waters.

Two families of squaliform sharks, the bramble sharks (Echinorhinidae) and the dogfish sharks (Squalidae) are present in the Fisher/Sullivan shark fauna.

#### Family Echinorhinidae Gill 1862a Genus *Echinorhinus* Blainville 1816

Bramble sharks are robust sharks that are most easily recognized by the numerous enlarged dermal thorns embedded in the skin (Figure 2.2). They have a homodont cutting dentition, with obliquely angled teeth that change little in size or shape along the jaws (Pfeil, 1983).

Bramble sharks are primarily benthic, deepwater sharks that are found in tropical and temperate waters at depths of

400-900 m. However, like cow sharks, they are known to occasionally enter shallower water. The diet consists of small bottom-dwelling bony fishes, sharks and invertebrates. They can reach body lengths of up to 4 m (Castro, 1983; Compagno, 1984; Steel, 1985)

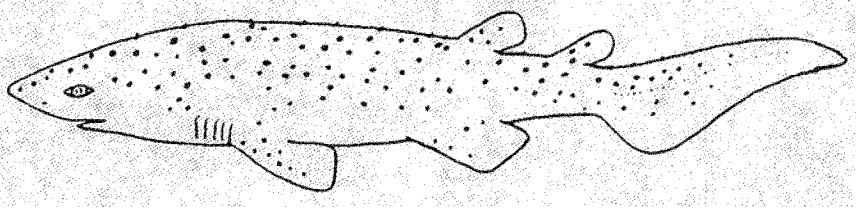


Figure 2.2. Bramble shark.

#### *Echinorhinus priscus* Arambourg 1952d Figured Specimens: Plate 2.1D-F.

**Description:** Teeth with a crown that is highly compressed and strongly inclined toward the distal margin. The coronal cutting edges are typically smooth, although they may be weakly serrate in some specimens. The mesial and distal shoulders either have only vestigial cusplets, or lack them altogether. The root is markedly compressed with a rectangular outline and two or three medial nutrient grooves. The maximum tooth width is about 12 mm.

The dermal thorn is a small, tetrahedral cone with a slender apex. The surface of the thorn has about seven longitudinal folds that form conspicuous projections on the basal margin when viewed apically. The basal surface is weakly convex. The illustrated thorn has a height of 1.7 mm.

**Remarks:** *E. priscus* teeth differ most noticeably from extant species in the form of the cusplets. Extant species typically have large, conspicuous cusplets, while in *E. priscus* the cusplets are greatly reduced or absent. However, these reduced cusplets are consistent with the lack of cusplets in the ancestral *Echinorhinus* from Cretaceous formations (Cappetta, 1987).

As with the hexanchids, the echinorhinids are primarily deepwater sharks, and this is the likely reason for the rarity of *E. priscus* in the Fisher/Sullivan site.

*E. priscus* is a poorly known shark. The only other record of this species is from the early Eocene phosphate beds of Morocco (Pfeil, 1983). The teeth from the Fisher/Sullivan Bone Bed are comparable to those illustrated in Pfeil (1983), except for the presence of serrations on some specimens. Despite this variability, the Fisher/Sullivan Bone Bed specimens probably represent a single species, since similar levels of variation are known in other *Echinorhinus* species (Pfeil, 1983).

#### Family Squalidae Bonaparte 1834

The dogfish sharks are generally small sharks, with

widely spaced, spined dorsal fins (Figure 2.3). Dentitions of these sharks can vary widely from homodont to dignathic heterodont conditions. In homodont dentitions, there are similar, strongly-inclined cutting teeth in both jaws, that change little in form along the jaws (Kent, 1994). Symphyseal teeth are present, but are asymmetrical and not easily distinguished from the other teeth when collected as isolated specimens (Cappetta, 1987). Dignathic heterodont dentitions have narrow, fang-like grasping teeth in the upper jaw, and broad triangular or oblique cutting teeth in the lower jaw. Symphyseal teeth can be either asymmetrical or symmetrical, depending on the species being examined (Cappetta, 1987).

Like the bramble sharks, squalids are primarily deepwater species that occasionally range into shallower water. Dogfish sharks eat a broad range of foods, including bony fishes, sharks, cephalopods, crustaceans, and marine mammals. Most dogfish are less than 1 m in length (Castro, 1983; Compagno, 1984; Steel, 1985).

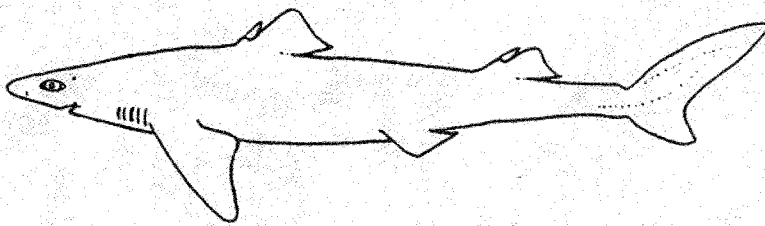


Figure 2.3. Dogfish shark.

**Genus *Squalus* Linnaeus, 1758**  
***Squalus crenatidens* (Arambourg, 1952D)**

**Figured Specimens: Plate 2.1G.**

**Description:** Teeth have a strongly-angled, compressed crown with coarsely serrate cutting edges. The mesial cutting edge is long and weakly convex to sigmoidal. The distal cutting edge meets the weakly convex distal enameloid shoulder at an acute angle in a distinct notch. The apron is long with subparallel sides and a rounded basal end that extends past the basal margin of the root. The compressed root is typical for the genus, with a large medio-lingual pore and a distinct uvula. Teeth of this species are typically about 4 mm wide.

**Remarks:** *S. crenatidens* is previously known only from Morocco (Arambourg, 1952), where it has been reported from early Paleocene through early Eocene horizons. The specimens from the Fisher/Sullivan Bone Bed differ from those illustrated by Arambourg in having somewhat coarser serrations, a less convex distal shoulder and a broader coronal apex. They may represent a separate species, although this will require a detailed comparison with Moroccan specimens.

Curiously, the widely distributed North Atlantic species, *S. minor*, has not been found in the Fisher/Sullivan Bone Bed. *S. minor* has been previously found in both the Paleocene and early Eocene of Europe (Cappetta, 1987), but it has been found only in the Paleocene beds of the Chesapeake Bay area (Ward and Wiest, 1990; Kent, 1994). The reasons for the absence of this species in the Chesapeake Bay area Eocene are unknown.

The dorsal fin spines that characterize the dogfish sharks are typically smooth and unornamented (Plate 2.1H).

**Genus *Isistius* Gill, 1864A**  
***Species *Isistius triturator* (Probst, 1979A)***

**Figured Specimen: Plate 2.1I.**

**Description:** The lower teeth are highly compressed, with broad, triangular crowns and rectangular roots. The crown is nearly equilateral and has smooth cutting edges that sometimes have extremely weak, undulating serrations. The apron is very short and nearly as broad as the basal margin of the crown. The root is roughly square in labial or lingual view and has a large, elliptical hole, just basal to the apron, that passes completely through the root. On the lingual face of the root, between this hole and the basal margin of the enameloid, is a large, roughly circular nutrient pore. The basal margin of the root is straight and lacks a flattened basal surface. Teeth typically about 5 mm wide.

**Remarks:** *I. triturator* is an Atlantic species, having been previously reported from late Paleocene through late Eocene sediments of Europe, Russia, Uzbekistan, Morocco, and the Chesapeake Bay region (Cappetta, 1987; Nolf, 1988; Ward and Wiest, 1990; Case, et al., 1996).

Cookiecutter sharks (*Isistius*) are small, pelagic species up to 50 cm in length, with reduced fins, large, triangular lower teeth and lips adapted for attachment (Figure 2.4). They feed by biting lumps of flesh from large bony fishes, sharks, dolphins, and whales. Their characteristic bite marks have also been reported from the rubber sonar housings of nuclear submarines (Compagno, 1984).

Cookiecutter sharks have a dignathic heterodont dentition of slender upper teeth and erect, triangular lower teeth (Cappetta, 1987). The delicate upper teeth of *I. triturator* have not been collected as fossils.



Figure 2.4. Cookiecutter shark.

**Order Squatiniformes Buen 1926**  
**Family Squatinidae Bonaparte 1838**  
**Genus *Squatina* Duméril 1906**

The angel sharks (family Squatinidae) have a highly depressed body and superficially resemble skates and rays. Unlike the true rays, the enlarged pectoral fins are not fused to the head (Figure 2.5). The homodont dentition consists of simple, slender clutching teeth (Kent, 1994).

Angel sharks are nearshore, benthic sharks in tropical and temperate waters, where they feed primarily on bottom-dwelling fishes and invertebrates. Angel sharks reach body lengths of about 2 m (Bigelow and Schroeder, 1948; Castro, 1983; Compagno, 1984).

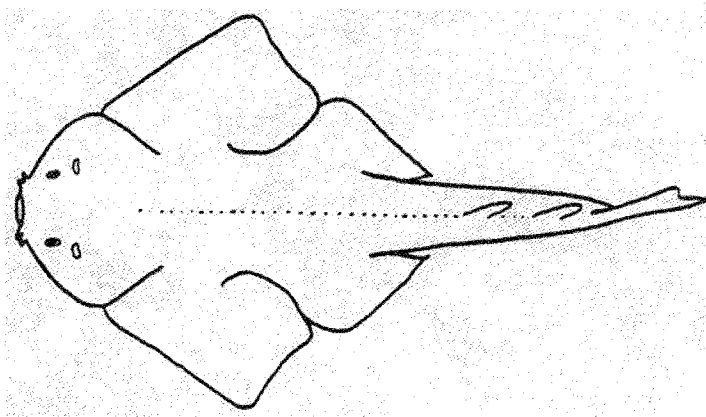


Figure 2.5. Angel shark.

*Squatina prima* (Winkler 1874)

**Figured Specimen:** Plate 2.1J.

**Description:** Teeth relatively wide with a slender, erect crown and smooth cutting edges that extend out onto long, nearly horizontal, enameloid shoulders. The surface of the crown is smooth, with a strongly convex lingual face and a weakly convex labial face. The apron is short and narrow, but extends below the basal margin of the root. The root is flattened and perpendicular to the crown when viewed in profile. The lingual protuberance is pronounced and has enameloid covering the apical surface. Anterior teeth are taller than lateral teeth and have a weakly concave, rather than flattened, basal surface of the root. The largest specimens are about 7 mm wide.

**Remarks:** *S. prima* has been previously reported from the early Paleocene through late Eocene of Morocco, England, and Belgium (Arambourg, 1952; Nolf, 1988; Kemp et al., 1990), the middle Eocene of South Carolina (Timmerman and Chandler, 1995), and the Paleocene and early Eocene of the Chesapeake Bay area (Ward and Wiest, 1990).

**Order Heterodontiformes Berg 1937**  
**Family Heterodontidae Gray 1851**  
**Genus *Heterodontus* Blainville 1816**

The bullhead sharks are small, benthic sharks with a cylindrical body and a blunt, rounded snout. The fins are relatively large and the two dorsal fins are each attached to a stout fin spine that acts as a cutwater (Figure 2.6). Bullhead sharks have a clutching-crushing dentition, consisting of anterior clutching teeth with small, sturdy cusps and cusplets, and large posterior crushing teeth with massive, domed crowns (Kent, 1994).

Although living species are known only from the Indo-Pacific region (Compagno, 1984), fossil species are also known from the Atlantic region (Nolf, 1988; Kemp, et al., 1990; Kent, 1994). Heterodontids have a cylindrical body, a short, blunt head, and two large, spined dorsal fins. They feed primarily on a variety of benthic invertebrates (e.g., sea urchins, crustaceans, mollusks and worms) and occasionally small, benthic fishes (Castro, 1983; Compagno, 1984).

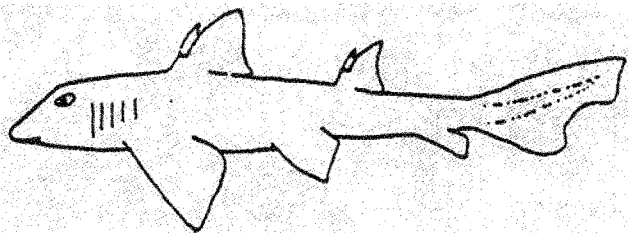


Figure 2.6. Bullhead shark.

*Heterodontus lerichei* Casier 1943

**Figured Specimens:** Plate 2.1K-L.

**Description:** The anterior teeth are small and stout, with an erect crown flanked by a single, sometimes poorly developed, cusplet on each shoulder. The enameloid almost completely overhangs the labial face of the root as a broad, bifurcated apron, and is smooth, except for some coarse wrinkles on the apron. The root is short with widely divergent lobes. The large lingual protuberance is covered with enameloid on the apical surface and has a conspicuous medial nutrient pore. A large nutrient pore is also located on the basal face of the root. Anterior teeth are small, with typical specimens about 3.5 mm tall.

Posterior teeth are very wide, with a low, domed crown. The apical surface of the crown has a conspicuous transverse crest extending along the entire width of the tooth. The enameloid surface of the crown is covered with delicate, closely-packed, anastomosing wrinkles, running roughly perpendicular to the crest. These wrinkles are strongest where they join the crest and become progressively weaker and more intricately branched toward the

basal margins of the crown. The root is short and greatly reduced, with a flattened basal face. Both the labial and lingual surfaces of the root have a single nutrient pore. Posterior teeth are much larger than anterior teeth, with a maximum width of about 20 mm.

**Remarks:** The original description of *H. lerichei* (Casier, 1943) was based on two posterior teeth, so the exact form of the anterior teeth is unknown. The anterior tooth illustrated here is provisionally placed in *H. lerichei*, since no other *Heterodontus* species has been found in the Fisher/Sullivan Bone Bed. The illustrated specimen is missing the root structure, which is presumably typical for the genus. The figured specimen differs from that shown in Kent (1994; fig. 7.1A), in having a shorter crown, less clearly defined cusplets and more extensive wrinkles on the labial face of the enameloid, although both probably represent the same species.

*H. lerichei* has been previously reported from the type locality in the Paleocene of Belgium (Casier, 1943) and the Paleocene and early Eocene of Maryland (Ward and Wiest, 1990). The Fisher/Sullivan Bone Bed posterior teeth bear some resemblance to the teeth of *H. vincenti* illustrated by Nolf (1988) from the middle Eocene of Belgium, but have consistently more closely spaced wrinkles.

### Order Orectolobiformes Applegate 1972

The carpet sharks (order Orectolobiformes) are a very diverse group. Many representatives are small, benthic sharks that are most abundant in shallow water, nearshore habitats. But the order also contains the pelagic, filter-feeding whale sharks, the largest living fish.

### Family Ginglymostomidae Gill 1862a

Nurse sharks in the family Ginglymostomidae are benthic, nearshore sharks of warm temperate and tropical waters. The body is elongate and cylindrical, with two spineless dorsal fins placed well back on the body, and a strongly heterocercal caudal fin (Figure 2.7). The blunt head has sensory barbels and a small mouth with short jaws and a homodont clutching dentition (Kent, 1994). The diet includes small benthic invertebrates and fishes (Castro, 1983; Compagno, 1984).

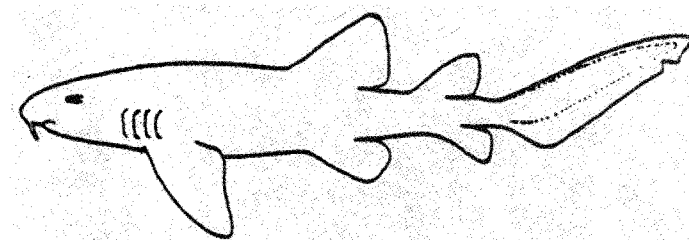


Figure 2.7. Nurse shark.

### Genus *Ginglymostoma* Müller and Henle 1837

The robust clutching teeth of *Ginglymostoma* have a large medial cusp and enameloid shoulders each bearing from one to ten cusplets. Anterior teeth are erect and symmetrical, with the teeth becoming lower and increasingly inclined distally. The apron is broad and moderately large, but does not reach the basal margin of the root viewed in profile. In some species, the basal margin of the apron is medially concave. The root is short with a flattened basal face that is semicircular in basal view. The basal surface bears a medial nutrient pore. One or more pairs of lateral nutrient pores are also present on the mesial and distal faces of the root.

### *Ginglymostoma africanum* Leriche 1927b

**Figured Specimen:** Plate 2.1M.

**Description:** Anterior teeth with a stout, erect crown and a single robust cusplet on each shoulder. Each cusplet has a broadly triangular, divergent apex and a vertical lateral margin. The apron is broad and sturdy with a smooth, unornamented surface, and a basal margin that is straight or weakly concave. The short root is typical for the genus and has a flat basal surface, a large basal pore and one or more lateral pores. Typical specimens are 4 mm tall.

Lateral teeth are nearly identical to anterior teeth, but have a modestly inclined cusp.

**Remarks:** The teeth of *G. africanum* are not easily confused with those of the other three nurse shark species from the Fisher/Sullivan Bone Bed. The presence of only a single cusplet on each shoulder of *G. africanum* is distinctive and clearly separates this species from *G. subafricanum*, *G. serra*, and *N. thielensis*.

*G. africanum* has a relatively restricted distribution, having been reported previously from the late Paleocene of the eastern United States and western Africa (Arambourg, 1952; Cappetta, 1987; Case, 1994; Kent, 1994). The specimens recovered from the Fisher/Sullivan Bone Bed are the first known from the Eocene.

### *Ginglymostoma subafricanum* Leriche 1927b

**Figured Specimen:** Plate 2.1N.

**Description:** Tooth with a short, erect crown and a pair of cusplets on each shoulder. Each cusplet has a broad base and a slender, divergent apex. The secondary cusplets are markedly smaller than the primary pair. The apron is large and broadly convex, with a smooth, unornamented surface. The abbreviated root is typical for the genus, with a flat basal surface, a large basal pore, and one or more lateral pores. Typical specimens have a height of 5 mm.

**Remarks:** The teeth of *G. subafricanum* are intermediate in morphology between *G. africanum* at one extreme and *G. serra* and *N. thielensis* at the other. However, the presence of a pair of slender, divergent cusplets on each shoulder of *G. subafricanum* is diagnostic within the Fisher/Sullivan Bone Bed. *G. subafricanum* has been previously reported from the early Paleocene of Morocco (Arambourg, 1952), the early and late Paleocene of Maryland (Ward and Wiest, 1990; Kent, 1994) and the late Paleocene and early Eocene of Mississippi (Case, 1994).

***Ginglymostoma serra* (Leidy 1877a)**

**Figured Specimen:** Plate 2.1O.

**Description:** *Ginglymostoma* teeth with a compressed, moderately prominent crown flanked on each side by four or more cusplets. The cusplets on each cutting edge are of graded sizes, with the largest immediately adjacent to the main cusp. The mesial cutting edge is straight to slightly convex, while the distal cutting edge is straight to slightly concave. The apron is broad with a weakly concave basal margin and a smooth unornamented surface. The root is short, with a flattened basal surface. There is a single, large basal nutrient pore and one or more pairs of lateral pores. Teeth usually about 5 mm tall.

**Remarks:** The teeth of *G. serra* are markedly different from those of the preceding species, having both a more compressed crown and a larger number of cusplets that form a distinct cutting edge. Consequently, this species is more easily confused with the next species, *Nebrius thielensis*, than with its sister species, *G. africanum* and *G. subafricanum*.

*G. serra* has a restricted range, having only been recorded from the early Eocene of the Chesapeake Bay region (Kent 1994), and the middle to late Eocene of Alabama (Thurmond and Jones, 1981).

**Genus *Nebrius* Rüppell 1837**  
***Nebrius thielensis* (Winkler 1873)**

**Figured Specimen:** Plate 2.1P.

**Description:** Asymmetrical teeth with five or more cusplets on each shoulder that are only slightly smaller than the strongly inclined main cusp. The cusplets are of graded size, with the largest proximal to the main cusp. The mesial cusplets form a strongly convex cutting edge, while those of the distal shoulder form a weakly convex edge. The apron is large and deep, extending below the basal root margin when the tooth is viewed in profile. The surface of the apron is smooth and unornamented and the basal edge is broadly rounded. The root is short with a flat base. The basal face

of the root has a large medial nutrient pore and two or more pairs of lateral pores. The largest teeth are about 8 mm tall.

**Remarks:** The teeth of *N. thielensis* resemble those of *G. serra* discussed above. However, the teeth of *N. thielensis* are distinguished by being more compressed, with a relatively smaller main cusp that is inclined toward the commissure, more numerous cusplets, and by a deeper apron that extends below the basal face of the root.

*N. thielensis* is a north Atlantic species, having been previously reported from the early through late Eocene of Belgium, England, Georgia, Mississippi, North Carolina and Virginia (Case, 1981, 1994; Weems, 1984; Nolf, 1988; Kemp, et al., 1990; Ward and Wiest, 1990; Kent, 1994; Timmerman and Chandler, 1995).

**Family Rhincodontidae Garmen 1913**

Whale sharks have large (up to 18 m long), streamlined bodies, large lunate tails, and large terminal mouths (Figure 2.8). They are pelagic, warm temperate to tropical sharks that have reduced the dentition to huge numbers of tiny hooked teeth. The teeth are not used directly for feeding, but serve primarily to retain small crustaceans and other zooplankton that have been filtered from the water by the denticle-covered esophageal papillae and cartilaginous rods on the gill arches (Bigelow and Schroeder, 1948; Compagno, 1984).

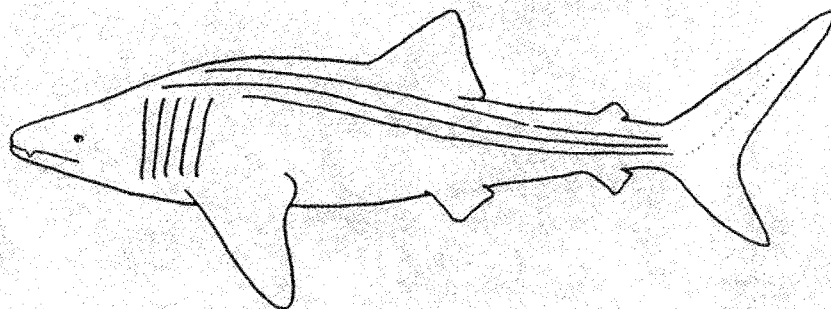


Figure 2.8. Whale shark.

**Genus *Palaeorhincodon* Herman 1974**  
***Palaeorhincodon wardi* Herman 1974**

**Figured Specimen:** Plate 2.1Q.

**Description:** Small teeth with a stout, lingually-inclined cusp and a pointed cusplet on each shoulder. Both the labial and lingual faces of the main cusp are smooth and strongly convex. The apron is broad, but very short, and does not reach the basal margin of the root. The root is globular, with a prominent lingual protuberance, that is covered on its apical surface with a broad veneer of smooth enameloid. The basal face of the root is trapezoidal in outline and has a medial nutrient pore in a broad nutrient groove that expands labially. A pair of marginal nutrient pores are also present. Teeth are small with a maximum height of about 3 mm.

**Remarks:** *P. wardi* has been previously recorded from the early to middle Eocene of Belgium, Morocco, Togo, and the late Paleocene of the Chesapeake Bay region (Cappetta, 1987; Kent, 1994). The tooth shown here is one of the first known specimens from the Eocene of the Chesapeake Bay area.

### Family Orectolobidae Jordan and Fowler 1903 Indeterminate Genus and Species

**Figured Specimen:** Plate 2.1R.

**Description:** Small tooth with a low, symmetrical crown. The short crown has long, sigmoidal cutting edges exhibiting coarse, irregular serrations that fade at either extremity. The lingual surface of the crown has a distinct medial ridge flanked on either side by slight depressions. The apron is of moderate size, with tapering margins and a broadly rounded basal end. It is relatively short and only extends very slightly below the basal margin of the root. The root is shallow, with a flattened basal surface. The lingual protuberance is comparatively small and has a large, circular pore in a broad nutrient groove. The apical half of the root surface on either side of the lingual protuberance is markedly excavated. A few inconspicuous marginal nutrient pores are scattered over the labial and lingual surfaces of the root. The maximum tooth dimension is 6 mm.

**Remarks:** Based on an examination of a photograph of this tooth, Cappetta (personal communications with R. Weems) tentatively identified this specimen as a symphyseal tooth from an unidentified squaliform shark. This identification seems unlikely. While symphyseal teeth do occur in the squaliforms, their shapes are inconsistent with that of the Fisher/Sullivan specimen. Of the squaliform subfamilies known or suspected to have symphyseal teeth, one (Squalinae) has asymmetrical teeth virtually identical to the other teeth in the jaws, one (Etmopterinae) has symmetrical teeth with a slender crown and numerous long, slender cusplets and two (Oxyrinotinae and Dalatiinae) have symmetrical teeth with tall, lanceolate crowns and deep rectangular roots (Compagno, 1984; Cappetta, 1987). None of these subfamilies exhibit the low, symmetrical blade-like crown and shallow root that characterizes the Fisher/Sullivan Bone Bed specimen.

More plausible taxonomic affinities of this tooth are likely to be found among the carpet sharks (Orectolobidae). The overall morphology of this tooth is reminiscent of some extinct orectolobids, most notably the genus *Cretorectolobus*, that have evolved a squatinid-like tooth morphology. *Cretorectolobus* teeth have the same low, stout crown with sigmoidal cutting edges and prominent apron as the specimen described here. Further, some lateral *Cretorectolobus* teeth even bear coarse serrations on the

enameloid shoulders. However, the specimen described here differs from *Cretorectolobus* in being generally more compressed and having a less pronounced lingual protuberance. This causes the basal root surface in the Fisher/Sullivan Bone Bed specimen to have a rectilinear profile, rather than the triangular outline normally seen in *Cretorectolobus* (Case, 1978; Cappetta, 1987).

Since only a single specimen of this shark is known, a more precise taxonomic assignment is inadvisable at this time. Additional specimens are needed to provide a clearer understanding of the range of variability inherent in this species.

### Order Lamniformes Berg 1958

Many of the largest and most conspicuous teeth from fossil sharks in the Fisher/Sullivan Bone Bed belong to members of the order Lamniformes. The lamniforms can be divided into two relatively distinctive groups, based on tooth and body morphology (Compagno, 1990; Kent, 1994). The narrow-tooth lamniforms are comparatively sluggish benthic sharks, with robust bodies and short, broad pectoral fins. They use slender, awl-like teeth to feed predominantly on bottom-dwelling prey. The broad-toothed lamniforms are more typically active, pelagic sharks, possessing more highly streamlined bodies and long slender pectoral fins. The generally broader teeth of these forms are capable of handling a larger size range of prey species.

### Family Odontaspidae Müller and Henle 1839

The sand tiger sharks (family Odontaspidae) are common benthic sharks with pointed snouts and large, slender teeth (Figure 2.9; Castro, 1983; Compagno, 1984). Odontaspids live in cool temperate waters, where they feed on a variety of fishes and invertebrates, such as squid and shrimp. Although relatively sluggish, they are capable of feeding on active prey.

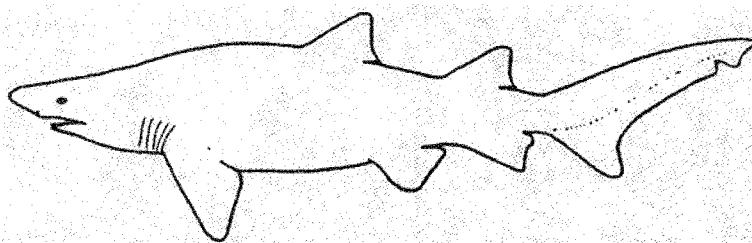


Figure 2.9. Sand tiger shark.

Considerable confusion surrounds the identification of fossil sand tigers, since species are moved around among different genera, seemingly at random. The extant species, *Carcharias taurus*, has been assigned to the genera *Odontaspis* (Castro, 1983), *Eugomphodus* (Compagno, 1984) and *Synodontaspis* (Cappetta, 1987). Research by

Glückman (1964a & b, 1967) and Compagno (1984) has clarified much of the confusion, by establishing that the genera *Carcharias* and *Odontaspis* represent ancient and distinct lineages of odontaspids. The reinstatement of *Carcharias* as a valid genus (International Commission on Zoological Nomenclature, 1987; Opinion 1459) has also reduced *Eugomphodus* and *Synodontaspis* to junior synonyms.

In addition to the two extant genera of sand tigers (*Carcharias* and *Odontaspis*) in the Fisher/Sullivan site, two additional extinct genera (*Striatolamia* and *Palaeohypotodus*) are also present.

One difficulty in evaluating the odontaspids from the Fisher/Sullivan Bone Bed is the disposition of teeth referable to the species *Pseudodontaspis lauderdalensis* and *P. mississippiensis*. Case (1987) erected the genus *Pseudodontaspis* for small odontaspids from the late Campanian through early Eocene that are distinguishable by having a striate crown with complete cutting edges, the presence of a long, deeply incised nutrient groove, and a more or less distorted root structure. In a later paper on the late Paleocene and early Eocene selachian fauna of Mississippi (Case, 1994), the species *P. lauderdalensis* and *P. mississippiensis* were named.

Unfortunately, the establishment of new taxa based solely on small specimens is always problematical, since they may simply reflect early ontogenetic stages of known species. The problem is further complicated in many shark families by the presence of parasymphyseal and intermediate teeth. The deformed roots that are frequently present on such teeth are disturbingly similar to the roots that are diagnostic for *Pseudodontaspis*. Pending a critical reevaluation of *Pseudodontaspis*, specimens otherwise attributable to this genus will be listed as parasymphyseal or intermediate teeth of indeterminate odontaspid species.

In overall form, specimens referable to *P. lauderdalensis* are strikingly similar to odontaspid intermediate teeth, which can resemble diminutive examples of either anterior or lateral teeth, but with distorted roots. Specimens matching the description of *P. mississippiensis* have largely undeformed roots, and most closely resemble odontaspid parasymphyseal teeth. Curiously, lateral teeth referable to *P. mississippiensis* have not been found in either the Mississippi type locality or the Fisher/Sullivan Bone Bed. The absence of such teeth would be consistent with their identification as parasymphyseals.

**Genus *Odontaspis* Agassiz 1838**  
***Odontaspis winkleri* Leriche 1905**

**Figured Specimens:** Plate 2.1S-T.

**Description:** Anterior teeth with a tall, slender crown and incomplete cutting edges that are restricted to the apical region. Two pairs of cusplets that are weakly divergent to nearly erect are present on the enameloid shoulders. In

some specimens, the tips of the primary cusplets may arch slightly toward the crown. Secondary cusplets are reduced, although less so, in juvenile specimens. The enameloid is completely smooth and overhangs the labial face of the root. The root has long, slender lobes with pointed or rounded tips and a pronounced lingual protuberance. The lingual protuberance is bisected by a deep, medial nutrient groove. Maximum size is about 25 mm.

Lateral teeth are shorter and wider than anterior teeth. The crown is not as tall as in anterior teeth, but is still slender with incomplete cutting edges. Three pairs of long, erect cusplets are present. The secondary cusplets are relatively large, but the tertiary cusplets are typically reduced. As in anterior teeth, the enameloid is smooth and noticeably overhangs the labial face of the root. The root lobes are slender, diverge at an obtuse angle, and have rounded tips. The lingual protuberance is less conspicuous, but retains the deep nutrient groove found in anterior teeth.

Posterior teeth are similar to lateral teeth, but have an even shorter crown and more widely divergent root lobes.

**Remarks:** *O. winkleri* is presently known from Europe, Central Asia, Maryland and Virginia (Eastman, 1901; Ward and Wiest, 1990; Cappetta, 1987; Kent, 1994; Timmerman and Chandler, 1995; Case, et al., 1996). The teeth of *O. winkleri* are rather delicate, suggesting that this shark fed on soft or weakly armored prey, such as the small fishes, squid, and shrimp eaten by extant members of this genus (Castro, 1983; Compagno, 1984).

**Genus *Carcharias* Rafinesque 1810**  
***Carcharias hopei* (Agassiz 1843)**

**Figured Specimen:** Plate 2.1U.

**Description:** Anterior teeth with a tall, moderately slender crown that is sigmoidal in profile. The cutting edges are nearly complete, ending a short distance apical to the cusplets. One pair of talon-like cusplets distinctly bent toward the crown are present on the enameloid shoulders. The enameloid is smooth, or with a very few extremely weak striations on the lingual face. The enameloid also overhangs the labial face of the root. The root has long, slender lobes with pointed or rounded tips and a strong lingual protuberance with a weak nutrient groove. Maximum size is about 40 mm.

Lateral teeth are shorter and wider than anterior teeth. The crown is more strongly compressed and inclined than that of anterior teeth, and has complete cutting edges. The primary cusplets are erect and triangular, and a small secondary pair may be present. As with the anterior teeth, the enameloid is smooth and overhangs the labial face of the root. The root has slender, strongly divergent lobes with rounded tips. The lingual protuberance is more modest, and has a nutrient groove similar to that of the anterior teeth.

**Remarks:** *C. hopei* has been found in a number of Paleocene and Eocene localities, including England (Casier, 1966; Kemp, et al., 1990), Uzbekistan (Case, et al., 1996), Morocco (Arambourg, 1952), Alabama (Thurmond and Jones, 1981), Mississippi (Case, 1994), North Carolina (Timmerman and Chandler, 1995), and in the Chesapeake Bay region (Ward and Wiest, 1990; Kent, 1994).

The Fisher/Sullivan Bone Bed also contains very stout *Carcharias* teeth that are sometimes identified as *C. robustus* (Nolf, 1988; Case, 1994). Based on an associated set of teeth, Ward (1989) has argued that specimens identified as *C. robustus* are simply positional variants of *C. hopei*. Unfortunately, the taxonomic fate of these specimens is still unclear, since the stockier teeth described by Ward (1989) are not as robust as those usually identified as *C. robustus*. For the present, I have chosen to refer all of these to *C. hopei*, since I have been unable to find a site where *C. robustus* occurs in the absence of *C. hopei*.

#### *Carcharias teretidens* (Agassiz 1843)

**Figured Specimen:** Plate 2.1V.

**Description:** Small anterior teeth with a tall, moderately slender crown that is sigmoidal in profile and has nearly complete cutting edges. There is one pair of slender, slightly sigmoidal cusplets on the enameloid shoulders. The enameloid is smooth on the labial face of the crown and overhangs the root face. The enameloid of the lingual face bears numerous fine, sinuous striations. The root lobes are long and slender, with pointed or rounded tips diverging at a weakly acute angle. The lingual protuberance is of moderate size and has a weak nutrient groove. Maximum size is about 15 mm.

Lateral teeth are short and broad, with a more blade-like crown and complete cutting edges. The cusplets are broad and triangular and secondary cusplets are completely lacking. The labial enameloid is smooth, while that of the lingual face is distinctly striated. The root has moderately slender, strongly divergent lobes with rounded tips. The lingual protuberance is comparatively small with a weak nutrient groove.

**Remarks:** *C. teretidens* has been previously collected from early Paleocene through early Eocene sites in England, Belgium, New Jersey, Mississippi and the Chesapeake Bay area (Cappetta, 1987; Nolf, 1988; Case, 1994; Kent, 1994; Case, 1996).

*C. teretidens* teeth are easily confused with those of *S. macrota*. However, the teeth of *C. teretidens* are more strongly sigmoidal in profile and have taller, more slender cusplets than those of the latter species.

#### Genus *Palaeohypotodus* Glückman 1964 *Palaeohypotodus rutoti* (Winkler 1874)

**Figured Specimen:** Plate 2.2A

**Description:** Anterior teeth have a moderately tall, moderately compressed crown with complete cutting edges. Two (or rarely three) pairs of slender, lanceolate cusplets are present. The primary pair is large and conspicuous, while the others are greatly reduced. As with the lateral teeth, the enameloid is smooth except for wrinkles on the basal margin of the labial face where it overhangs the root. The root has long, slender lobes with rounded tips and a strong lingual protuberance with a deep nutrient groove. Largest specimens reach a height of about 30 mm.

Upper lateral teeth with a broad, compressed crown that is more blade-like than that of most other odontaspids. The cutting edges are complete. Two pairs of cusplets are present on enameloid shoulders, but while the primary cusplets are large and sharp, the secondary ones are vestigial. The enameloid is smooth, except for a series of short, vertical wrinkles along the basal margin, where the enameloid overhangs the labial face of the root. The root has slender, strongly divergent lobes with rounded tips. The lingual protuberance is reduced and has a deep nutrient groove.

**Remarks:** *P. rutoti* is an uncommon species in the Fisher/Sullivan Bone Bed. This species has been previously recorded from the Paleocene and early Eocene of Europe, New Jersey, the Chesapeake Bay region, and possibly, Morocco (Cappetta, 1987; Nolf, 1988; Ward and Wiest, 1990; Case, 1996).

#### Genus *Striatolamia* Glückman 1964 *Striatolamia macrota* (Agassiz 1843)

**Figured Specimens:** Plate 2.2B-D.

**Description:** Anterior teeth with tall, moderately slender and weakly sigmoidal crown and cutting edges that are nearly complete. A single pair of vestigial cusplets is typically present, although they may be absent in some specimens. The labial enameloid is smooth and overhangs the labial face of the root. The basal half of the lingual face of the crown is covered by slender, tightly packed striations. The root lobes are long and slender, with pointed tips diverging at a strongly acute angle. The lingual protuberance is of modest size and has a deep nutrient groove. Maximum size is about 45 mm.

Lateral teeth are shorter and have a much more compressed crown and complete cutting edges. The cusplets are broadly triangular to low and convex and may be weakly serrated in some specimens. The crown is smooth on the labial face and weakly striated to smooth on the lingual face. The root lobes are short and broad with spatulate tips. The lingual protuberance is weak and the lingual face of the root is beveled in profile. The nutrient groove is deeply incised into the lingual face of the root.

**Remarks:** *S. macrota* is a broadly distributed species, having been found in the early and middle Eocene of France, England, Belgium, Kazakhstan, Uzbekistan, Morocco, Alabama, Mississippi, North Carolina and the Chesapeake Bay region (Arambourg, 1952; Glückman, 1967; Thurmond and Jones, 1981; Cappetta, 1987; Nolf, 1988; Kemp, et al., 1990; Ward and Wiest, 1990; Case, 1994; Timmerman and Chandler, 1995; Case, et al., 1996)

#### Family Mitsukurinidae Jordan 1898

Mitsukurinids, or goblin sharks, have a flexible, compressed snout that projects anteriorly from the dorsal surface of the head (Figure 2.10). The most plausible function of this flexible snout is to aid in prey detection (Compagno, 1984). Sharks have specialized electroreceptors, the ampullae of Lorenzini, on the head that are used to detect the electrical impulses generated within the muscles of their prey. By spreading these receptors over the enlarged area of the snout, goblin sharks can rapidly search larger areas of substrate for buried prey. Extant goblin sharks (genus *Mitsukurina*) are deepwater sharks. The absence of light at the depths where living goblin sharks occur would make the ability to detect prey electrically, rather than visually, a tremendous advantage.

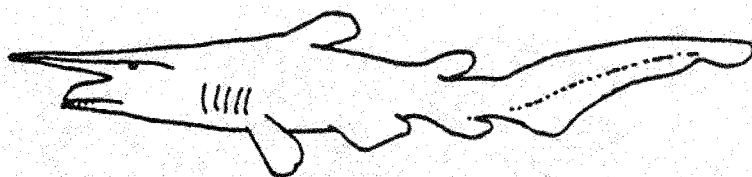


Figure 2.10. Goblin shark.

#### Genus *Anomotodon* Arambourg 1952 *Anomotodon novus* (Winkler 1874)

**Figured Specimens:** Plate 2.2E-F.

**Description:** Anterior teeth with tall, slender crowns. The cutting edges are complete and continue across the sloping enameloid shoulders to the basal margin of the enameloid. The surface of the enameloid is smooth, except for a few very weak, sinuous striations on the basal half of the lingual face of the crown. The root lobes are of modest length with rounded tips, and diverge at an acute to weakly obtuse angle. The lingual protuberance is of moderate size and bears a deep nutrient groove. The largest teeth are about 15 mm tall.

Lateral teeth have a shorter, broader crown. As with the anterior teeth, cusplets are lacking and the cutting edges simply extend out onto the shoulders. The enameloid is smooth, save for a few weak striations on the lingual face. The root lobes are shorter and broader than those of anterior teeth, and diverge at a larger angle. The lingual protuberance is reduced, but retains a deep nutrient groove.

The entire lingual surface of the root is beveled, producing a wedge-shaped profile.

**Remarks:** *A. novus* is an Eocene species previously found in Belgium, England, the former Soviet Union, and the Chesapeake Bay region (Cappetta, 1987; Kemp, et al., 1990; Ward and Wiest, 1990). This species is frequently placed in the genus *Isurus* (mako sharks); however, the presence of striations on the lingual face of the crown, the beveled lingual face of the root on lateral teeth, and the deep nutrient groove are all characteristics that are unknown in *Isurus*.

Case (1994) describes a contemporaneous, unnamed *Anomotodon* species from the late Paleocene and early Eocene of Mississippi. This species differs from the Fisher/Sullivan Bone Bed *A. novus* teeth in having the cutting edges on the enameloid shoulders elaborated into convex, nearly horizontal heels. In *A. novus* the shoulders are sloped, and comparatively straight.

#### Family Cretoxyrhinidae Glückman 1958

Mackerel sharks (Figure 2.11) are large lamnids with highly streamlined bodies and possessing teeth with pronounced lateral cusplets. Earlier workers tended to place all cuspletted lamnoid teeth into the genus *Lamna*. More recent research has delineated a number of distinct evolutionary lineages among fossil *Lamna* and this has led to the erection of a number of additional genera and families (Glückman, 1958, 1964a; Cappetta, 1976, 1987; Landemaine, 1991).

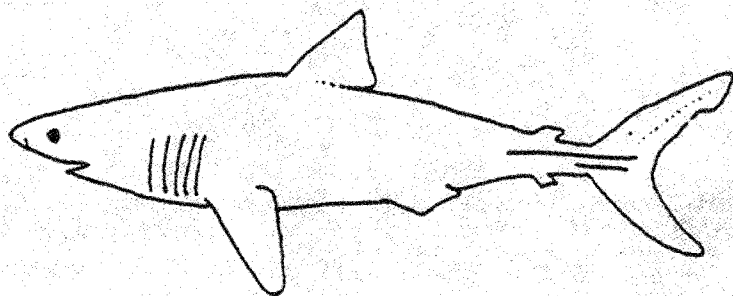


Figure 2.11. Mackerel shark.

#### Genus *Cretolamna* Glückman 1958 *Cretolamna appendiculata* (Agassiz 1843)

**Figured Specimens:** Plate 2.2G-H.

**Description:** Anterior teeth with a compressed, moderately tall and wide crown with complete, smooth cutting edges. There is a single pair of triangular, weakly divergent primary cusplets. The enameloid on both the crown and the cusplets is completely smooth. The basal groove is relatively narrow and inconspicuous. The root is

moderately robust and has a comparatively small lingual protuberance. The protuberance contains a cluster of several nutrient pores, but has, at best, only a weak nutrient groove. In many specimens, the nutrient groove is completely lacking. The root lobes are short and have rectilinear tips. The basal margin of the root consists of the roughly aligned margins of the lobes, separated by a distinctly U-shaped medial notch. Maximum tooth height about 30 mm.

Lateral teeth are similar to anterior teeth, but are shorter and wider. Both the crown and the cusplets are lower and broader. The root is less robust and more compressed. The root lobes are abbreviated, with vertical mesial and distal margins. The basal root margin is nearly horizontal, except for a broad, shallow basal concavity. The nutrient pores and nutrient groove are comparable to those of the anterior teeth.

**Remarks:** The systematics of the genus *Cretolamna* have yet to be clearly delineated. Although many species have been named, the level of morphological variation within most of these species is poorly understood. Recently, Landemaine (1991) erected the genus *Serratolamna* (family Serratolamnidae) for several species previously placed within *Cretolamna*.

*C. appendiculata* is the most cosmopolitan species within *Cretolamna*, and is the only representative of this genus in the Fisher/Sullivan Bone Bed. This species is essentially worldwide in distribution and has been found from the Late Cretaceous through the early Eocene in Europe, central Asia, northern and western Africa, Madagascar, Japan, Australia, New Zealand, Canada, Alabama, New Jersey, Delaware, Maryland, Virginia, North Carolina and Kansas (Arambourg, 1952; Applegate, 1970; Lauginiger and Hartstein, 1983; Cappetta, 1987; Case, 1989; Kent, 1994; Timmerman and Chandler, 1995; Case, et al., 1996).

#### **Family Serratolamnidae Landemaine 1991** **Genus *Serratolamna* Landemaine 1991**

The genus *Serratolamna* has been recently erected for some species formerly placed in *Cretolamna*. Characters separating *Serratolamna* from *Cretolamna* include (1) a marked tooth asymmetry, (2) multiple cusplets, and (3) a short nutrient groove (Landemaine, 1991). Anterior teeth may only have a primary cusplet, although there is frequently a tiny secondary cusplet present. Lateral and posterior teeth typically have a secondary cusplet on each shoulder and a tertiary cusplet on the distal shoulder. Several species have been transferred from *Cretolamna* to *Serratolamna*, but at present it is equivocal that these species form a monophyletic group.

#### ***Serratolamna aschersoni* (Stromer, 1905)**

**Figured Specimen:** Plate 2.2I.

**Description:** Anterior teeth having tall, broadly triangular crowns with smooth, complete cutting edges. A single triangular and weakly divergent primary cusplet is present on each shoulder. Both the crown and the cusplets are covered with smooth enameloid. A narrow basal groove separates the crown from the root, which has short root lobes with rounded tips. The comparatively small lingual protuberance has a single nutrient pore, that is sometimes located within a weak nutrient groove. The basal root margin is broadly concave to obtusely angled. Largest specimens are about 25 mm tall.

Lateral teeth have shorter, wider crowns, with a pronounced distal curvature. In addition to the large, divergent primary cusplets, one or two smaller, accessory cusplets are also typically present on each shoulder. As with the anterior teeth, a single nutrient pore, sometimes within a weak nutrient groove, is present. The root lobes are shortened and diverge at a strongly obtuse angle.

**Remarks:** *S. aschersoni* has a relatively restricted range, having been recorded from the early Eocene of Morocco (Arambourg, 1952), Mississippi (Case, 1994) and the Chesapeake Bay area (Kent, 1994).

#### ***Serratolamna lerichei* (Casier 1946)**

**Figured Specimens:** Plate 2.2J-K.

**Description:** Anterior teeth with a tall, moderately broad, compressed crown bearing complete cutting edges. One, or sometimes two, erect cusplets that have a broad base and taper to slender, delicate points are present on each shoulder. The enameloid is entirely smooth. The basal groove is narrow. The root has short lobes with rounded tips. The lingual protuberance is weakly elevated with a single nutrient pore that is frequently within a weak nutrient groove. The basal margin of the root is obtusely angled.

Lateral teeth are similar to anterior teeth, but are shorter, wider and more clearly asymmetrical. The primary cusplets are erect with slender tips. Two or three accessory cusplets are also present on each shoulder. The lingual protuberance is reduced and the root lobes are abbreviated.

**Remarks:** When Landemaine (1991) erected *Serratolamna*, *S. lerichei* was not among the species transferred to the new genus. Based on the evaluation of only a few specimens from the Fisher/Sullivan Bone Bed, Kent (1994) followed this assignment and retained this species within *Cretolamna*. However, based on a larger sample from the Fisher/Sullivan Bone Bed, this species consistently has the three major characters that are used to separate *Serratolamna* from *Cretolamna* — a distinctly asymmetrical crown, a tendency toward having multiple cusplets, and a short nutrient groove with a single nutrient pore. Given the presence of these characters, this species seems more appropriately placed in *Serratolamna*.

*S. lerichei* has been reported from the Paleocene through middle Eocene of England, Belgium, Uzbekistan, North Carolina, Mississippi, and the Chesapeake Bay region (Nolf, 1988; Kemp, et al., 1990; Carter et al., 1988; Ward and Wiest, 1990; Case, 1994; Case, et al., 1996).

**Family Otodontidae Glückman, 1964**

**Genus *Otodus* Agassiz 1843**

***Otodus obliquus* Agassiz 1843**

**Figured Specimens:** Plate 2.2L-M.

**Description:** The anterior teeth are massive, with tall, compressed, lanceolate crowns and complete cutting edges. A pair of large, triangular and divergent cusplets are also present and in some specimens, a pair of reduced secondaries may also occur. The basal groove is medially very broad, but becomes narrower toward the mesial and distal margins of the tooth. On well-preserved specimens, the basal groove may be covered with a thin layer of pallial dentine. The root is robust with a prominent lingual protuberance that lacks a nutrient groove. Nutrient pores are clustered on the most elevated portion of the protuberance, with a few additional pores scattered in an arc onto each root lobe. These pores are frequently permineralized and can be difficult to observe. The root lobes are relatively short with rounded tips. The basal margin of the root is deeply notched, rather than angled. Typical specimens are 60-70 mm tall.

Lateral teeth have crowns that are shorter, broader and more inclined than those of anterior teeth. As with anterior teeth, the cutting edges are complete, and a pair of large, divergent cusplets are present. Lateral teeth are more likely to have a pair of secondary cusplets than anterior teeth, although they are still considerably reduced in size, when compared to the primary cusplets. The basal groove is similar to that of anterior teeth, but is longer and slightly narrower. The root is robust, although the lingual protuberance is reduced. The distribution of nutrient pores resembles that of anterior teeth, although the number of pores may be reduced. The root lobes are short and have rounded tips.

**Remarks:** *O. obliquus* is the largest shark in the Fisher/Sullivan Bone Bed, and was probably the top carnivore in the assemblage. This species is very widely distributed in the Atlantic, having been found in the late Paleocene and early Eocene of France, Belgium, England, Bulgaria, Italy, Morocco, Angola, Zaire, New Jersey, Maryland, Virginia, North Carolina and Florida (Tessman, 1966; Case, 1985; Cappetta, 1987; Nolf, 1988; Kemp, et al., 1990; Ward and Wiest, 1990; Timmerman and Chandler, 1995).

Curiously, there are only two reports of *O. obliquus* from outside the Atlantic, and both purportedly from Miocene formations in the Pacific Ocean. One specimen was dredged in the Pacific off the coast of Russia (Glückman, 1964a),

while the second was collected from Japan (Hasegawa and Uyeno, 1967). The Russian specimen has a broad, triangular crown, triangular cusplets, a broad basal groove, and drooping root lobes that are all consistent with *Otodus*. However, since this tooth was dredged from the ocean bottom, there is some question as to the reliability of the stratigraphic assignment.

The Japanese specimen is morphologically quite different, with a tall, slender crown and a pair of broad cusplets, and is probably not referable to *Otodus* (Hideo Yabe, pers. comm.). Because both records of Miocene *Otodus* from the Pacific are questionable, it seems prudent to regard *O. obliquus* as a late Paleocene to early Eocene species, that is possibly restricted to the North Atlantic.

**Order Carcharhiniformes Compagno 1977**

The carcharhiniforms, or ground sharks, are the most diverse group among the eight extant orders of sharks, with over half of the living shark species (Compagno, 1984). Despite this success, the carcharhiniforms have a poor fossil record prior to the Miocene. The ground sharks in the Fisher/Sullivan Bone Bed are relatively primitive forms. The more advanced tooth morphologies that characterize many of the more successful living ground sharks, did not appear until the Neogene (Maisey, 1984).

**Family Scyliorhinidae Gill 1862**

Catsharks in the family Scyliorhinidae are the most diverse group of carcharhiniforms. They are very widely distributed from the tropics to the poles. Catsharks are small (up to 1.6 m long), benthic sharks, that occur from the intertidal zone to depths of at least 2000 m. Catsharks have long, slender bodies, with a pair of spineless dorsal fins and a single anal fin positioned well back on the body (Figure 2.12). Their small clutching teeth are used to capture small benthic invertebrates and fishes (Castro, 1983; Compagno, 1984).

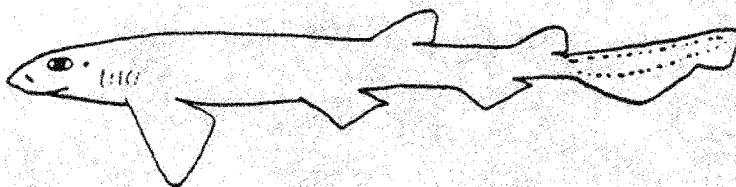


Figure 2.12. Catshark.

**Genus *Scyliorhinus* Gill 1862**

***Scyliorhinus gilberti* Casier 1946**

**Figured Specimen:** Plate 2.2N.

**Description:** Small anterior teeth, having a slender main cusp with incomplete to nearly complete cutting edges, and one, or more typically, two pairs of cusplets. The primary

cusplets are noticeably larger and more conspicuous than the secondary cusplets. The enameloid on the labial face of the crown markedly overhangs the labial face of the root and has strongly developed wrinkles along the basal margin. The root is short, with round, moderately abbreviated root lobes and a strongly beveled lingual face. There is a single medial nutrient pore within a deep nutrient groove on a distinct lingual protuberance. A pair of marginal nutrient pores are present on the flanks of the lingual protuberance. The largest teeth are about 3 mm tall.

Lateral teeth are similar to anterior teeth, but are wider and less elevated.

**Remarks:** *S. gilberti* has a restricted distribution, having been previously reported from the late Paleocene through late Eocene of Europe, the middle Eocene of central Asia, and the early Paleocene through middle Eocene of the Chesapeake Bay area (Cappetta, 1987; Ward and Wiest, 1990; Case, et al., 1996). The small size of this species, coupled with the deepwater habitats of many extant *Scyliorhinus*, is probably responsible for the rarity of this species in the Fisher/Sullivan Bone Bed.

**Genus *Premontria* Cappetta 1992**  
***Premontria degremonti* Cappetta 1992**

**Figured Specimen:** Plate 2.20

**Description:** Small anterior teeth, having a slender main cusp and a single pair of broad cusplets. The cusplets are somewhat variable in form, ranging from conspicuous to vestigial. The enameloid on the labial face of the crown clearly overhangs the root face and has numerous weakly developed striations along the basal margin. The root is comparatively deep, with compact root lobes and a beveled lingual face. There is a deep nutrient groove with a single medial nutrient pore. A pair of marginal nutrient pores are present on the lateral surfaces of the lingual protuberance. The largest teeth are about 5 mm tall.

Lateral teeth are similar to anterior teeth, but are wider and less elevated.

**Remarks:** *P. degremonti* has been previously reported from the Early Eocene of France (Cappetta, 1992). This species differs from the only other scyliorhinid in the Fisher/Sullivan Bone Bed, *S. gilberti*, in having fewer cusplets, finer basal wrinkles on the labial face of the crown, and a more globular root.

This is the first record of *P. degremonti* from the Western Hemisphere.

**Family Triakidae Gray 1851**

The houndsharks are small to medium-sized sharks (up to 2 m) with slender, elongate bodies, two widely separated, spineless dorsal fins, and an anal fin (Figure 2.13). They are

nearshore species, widely distributed in tropical and temperate waters, where they feed on a variety of bony fishes, cartilaginous fishes and invertebrates (Castro, 1983; Compagno, 1984).

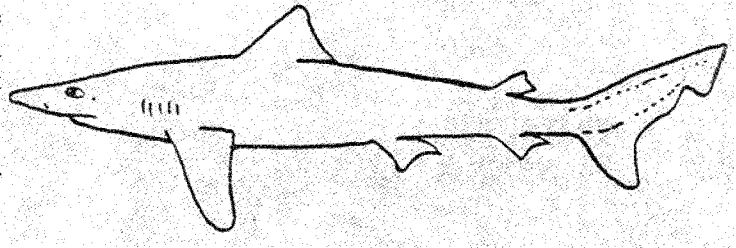


Figure 2.13. Houndshark

**Genus *Pachygaleus* Cappetta 1992**  
***Pachygaleus lefevrei* (Daimeries 1891a)**

**Figured Specimen:** Plate 2.2P.

**Description:** Moderately small teeth with an oblique, compressed crown. The mesial cutting edge is weakly convex, with smooth cutting edges. The distal cutting edge has four or more pronounced serrations that become smaller distally. The enameloid is generally smooth, although a few irregular wrinkles may be present where the labial face of the crown overhangs the root. The root is wide and moderately robust. The root lobes are abbreviated and have rounded extremities. The deep nutrient groove has a single nutrient pore and ends in a distinct notch in the basal margin of the root. Teeth of this species are relatively large, with maximum widths of about 10 mm.

**Remarks:** *P. lefevrei* has been previously reported from the Early and Middle Eocene of Europe and Maryland (as *Galeorhinus lefevrei*; Nolf, 1988; Kemp, et al., 1990; Kent 1994). Case (1994) lists this species from the Late Paleocene of Mississippi, but the illustrated specimens have significantly fewer distal serrations (2 vs. 6 or more) than the specimens of *P. lefevrei* shown by Nolf (1988) and Kemp, et al., 1990).

The teeth of *P. lefevrei* are similar to those of another triakid from the Fisher/Sullivan Bone Bed, *G. yresiensis*. Compared to this latter species, the teeth of *P. lefevrei* are generally larger, more robust and lack serrations on the mesial cutting edge.

**Genus *Galeorhinus* Blainville, 1816**  
***Galeorhinus yresiensis* Casier, 1946**

**Figured Specimen:** Plate 2.2Q.

**Description:** Small teeth with an elevated, compressed crown that is noticeably oblique. The mesial cutting edge is sigmoidal, and is weakly and irregularly serrate on the basal half. The distal cutting edge supports four or five distinct

serrations that become reduced in size away from the main cusp. The enameloid is generally smooth, although a few basal wrinkles may be present on the labial face where it strongly overhangs the face of the root. The root is wide and compressed. The root lobes are abbreviated and have mildly convex basal margins. There is a deep nutrient groove, with a single nutrient pore that forms a distinct gap in the basal margin of the root. Typical specimens are 6 mm wide.

**Remarks:** *G. ypresiensis* is uncommon within the Fisher/Sullivan Bone Bed. However, it does have a relatively wide distribution, having been found in the early to middle Eocene of Belgium, England, Maryland and Mississippi (Nolf, 1988; Kemp, et al., 1990; Ward and Wiest, 1990; Case, 1994).

**Genus *Triakis* Müller and Henle 1838a**  
***Triakis wardi* Cappetta 1976**

**Figured Specimen:** Plate 2.2R.

**Description:** Small tooth having a strongly angled crown with a sigmoidal cutting edge. The mesial shoulder is broadly rounded and lacks cusplets. The distal cutting edge is strongly convex with two poorly differentiated cusplets. The enameloid noticeably overhangs the labial face of the root and has a series of short, strong wrinkles along the basal margin. The enameloid of the lingual face is generally smooth, except for a few weak, oblique striations on the mesial shoulder. The root is comparatively short, with a flat basal face. There is a deep nutrient groove, containing a single medial nutrient pore, that meets the basal root margin as a conspicuous notch. Maximum tooth width is about 2 mm.

**Remarks:** The figured specimen is typical for the species, although there tends to be some variability in the development of the cusplets. In many specimens, the distal cusplets are tall and distinct. Some specimens also have a pair of cusplets on the mesial shoulder.

*T. wardi* has a restricted distribution, having been only previously reported from the early to middle Eocene of England (Kemp, et al., 1990).

**Genus *Palaeogaleus* Gurr 1962**  
***Palaeogaleus vincenti* (Daimeries 1888a)**

**Figured Specimen:** Plate 2.2S.

**Description:** The anterior teeth are small, with a broad, thick crown angled slightly toward the jaw commissure. Two, or sometimes three, pairs of weakly divergent cusplets are present. The labial face of the crown overhangs the root in a distinct bulge that usually bears a few short, vertical wrinkles. Wrinkles may also be present on the lingual face,

immediately basal to the cusplets, although they tend to be weaker than those on the labial face. The root is short and stout with a flat basal margin. The lingual protuberance is bisected by a large, conspicuous nutrient groove that forms a distinct notch in the basal root margin. A single large medial nutrient pore is located within the nutrient groove. Numerous small marginal nutrient pores are also present. The largest teeth are about 4 mm.

Lateral teeth are comparable in form to the anteriors, but are lower and wider, with up to four, weakly differentiated cusplets on each shoulder. In some specimens, the mesial shoulder lacks cusplets and forms a low, convex ridge. The root is less robust and has a mildly concave basal margin.

**Remarks:** This species has been previously reported from the Paleocene and Eocene of Belgium, France, England, Uzbekistan, Greenland and the eastern United States (Cappetta, 1987; Ward and Wiest, 1990; Kent, 1994; Case, 1996; Case, et al., 1996).

**Family Carcharhinidae Jordan and Evermann 1896**

The gray, or requiem, sharks (family Carcharhinidae) constitute one of the largest and most successful families of living sharks (Figure 2.14). They are most common in tropical waters, although they are well-represented in temperate climates, as well. They occupy a variety of environments, from coastal to pelagic, with many species specializing on particular habitats. Carcharhinids are typically large, active sharks capable of sudden bursts of speed for pursuing prey, although a number of smaller forms are also known. The diet is typically diversified, including bony and cartilaginous fishes, cephalopods, crustaceans, birds and marine mammals (Castro, 1983; Cappetta, 1987).

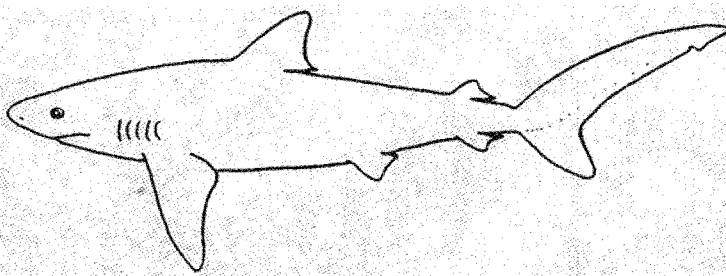


Figure 2.14. Gray shark.

**Genus *Abdounia* Cappetta 1980**

The extinct genus *Abdounia* contains carcharhinids with slender, lanceolate crowns and distinct cusplets on each shoulder. The teeth are generally small, with most teeth measuring 5 mm or less.

***Abdounia beaugei* (Arambourg 1935)**

**Figured Specimens:** Plate 2.3A.

**Description:** Small anterior teeth with moderately tall, erect crowns, and one or two broadly triangular, and typically divergent, cusplets on each shoulder. The coronal cutting edges are complete and adjoin those of the cusplets. The enameloid on the labial face of the crown is flat, and does not overhang the root, but is broadly contiguous with that of the cusplets. The enameloid of the weakly convex lingual face is equally devoid of sculpturing. The root is broad and somewhat compressed, with laterally extended lobes. The basal margin of each root lobe is weakly convex. The lingual face is beveled and bears a conspicuous nutrient groove that ends at the basal margin in a distinct, medial notch. The maximum size of these teeth is about 4 mm.

Lateral teeth are similar to anterior teeth, but have a crown that is distinctly angled to the rear. The mesial shoulder lacks cusplets, but may exhibit a long, low ridge. The distal shoulder has two, or in some cases three, triangular cusplets. The root is similar to that of anterior teeth, although rather more compressed. As with anterior teeth, the maximum size is about 4 mm.

**Remarks:** The small teeth of *A. beaugei* are a common, if inconspicuous component of the Fisher/Sullivan Bone Bed fauna. *A. beaugei* is a widely distributed North Atlantic species, having been previously reported from the middle Paleocene through middle Eocene of Morocco, Tunisia, England, France, Belgium, Uzbekistan, Maryland and Mississippi (Cappetta, 1987; Nolf, 1988; Ward and Wiest, 1990; Kemp, et al., 1993; Case 1994; Case, et al., 1996).

***Abdounia minutissima* (Winkler 1873)**

**Figured Specimen:** Plate 2.3B.

**Description:** Small anterior teeth with tall, slender crowns, and one erect, triangular cusplet on each shoulder. The coronal cutting edges are complete and continuous with those of the cusplets. The enameloid on the labial face of the crown is broadly contiguous with that of the cusplets, and does not overhang the labial face of the root. It is smooth, except for a few fine, basal striations on some specimens. The enameloid of the lingual face of the crown is likewise largely smooth, although scattered basal striations may be present. The root is wide and slightly compressed, with laterally prolonged lobes, each having a weakly convex basal margin. The lingual root face is beveled, with a pronounced medial nutrient groove that forms a conspicuous notch in the basal root margin. The maximum size of anterior teeth is about 4 mm.

Lateral teeth resemble anterior teeth, although the crown is shorter and somewhat less erect. Maximum size for lateral teeth is 4 mm.

**Remarks:** The teeth of *A. minutissima* are similar to those of *A. beaugei*. The primary differences between the two species are the taller, more slender crown and single pair of

cusplets in *A. minutissima*.

*A. minutissima* has a range restricted to the North Atlantic, having been reported from the early to middle Eocene of Belgium (Cappetta, 1987), England (Kemp, et al., 1990), Mississippi (Case, 1994; as *A. subulidens*), and possibly North Carolina (Timmerman and Chandler, 1995; as *A. lapierrei*).

***Abdounia recticon* (Winkler 1873)**

**Figured Specimens:** Plate 2.3C-D.

**Description:** Small teeth with moderately large, inclined crowns, and three or more triangular, divergent cusplets on each shoulder. The coronal cutting edges are complete and are continuous with those of the cusplets. The enameloid on the labial face of the crown is flat, and generally smooth. It slightly overhangs the labial face of the root and is ornamented with a few short vertical wrinkles along the basal margin. The enameloid of the lingual face is entirely smooth. The root is wide and slightly compressed. The basal margin of each root lobe is weakly convex. The lingual root face is distinctly beveled and has an obvious nutrient groove. The maximum height is about 5 mm.

**Remarks:** *A. recticon* is a rare member of the Fisher/Sullivan Bone Bed shark fauna. Specimens from this site exhibit considerable variation in cusplet number, from a minimum of three to a maximum of seven. White (1956) recognized two separate subspecies of *A. recticon* — *A. recticon recticon* (with three or four cusplets) and *A. recticon claibornensis* (with five to eight cusplets). *A. recticon recticon* has been previously recorded from the early to middle Eocene of Belgium, England, Uzbekistan, Maryland and Alabama (Thurmond and Jones, 1981; Nolf, 1988; Kemp, et al., 1990; Ward and Wiest, 1990; Case, et al., 1996). *A. recticon claibornensis* is a warmer water form known from Alabama, North Carolina, and the Chesapeake Bay region (Thurmond and Jones, 1981; Kent, 1994; Timmerman and Chandler, 1995).

Both tooth forms are present in the Fisher/Sullivan Bone Bed, but specimens are too rare to determine whether they represent distinct subspecies (or full species?), or simply extreme variants of a single, highly variable species.

**Genus *Physogaleus* Cappetta 1980**  
***Physogaleus secundus* (Winkler 1874)**

**Figured Specimens:** Plate 2.3E-F.

**Description:** Moderately small anterior teeth with a long, angled crown and complete cutting edges. The crown may be compressed and relatively broad, with a convex mesial cutting edge, or slender and less compressed with a sigmoidal edge. The enameloid is completely smooth, and on the labial face slightly overhangs the face of the root. The

mesial cutting edge is typically smooth, although a few irregular serrations may be present on the basal third. The distal shoulder usually has one or more, somewhat larger serrations. The root is wide and slightly to markedly robust. The root lobes are elongated laterally, with weakly convex basal margins. The lingual root face is clearly beveled, with a deep nutrient groove that forms an obvious notch in the basal margin of the root. The maximum size of anterior teeth is about 7 mm.

Lateral teeth resemble anterior teeth, although the crown is distinctly broader and more compressed. The mesial cutting edge may be completely smooth, but more usually has several serrations on the basal half of the crown. The distal shoulder has a low, convex ridge that frequently exhibits several uneven serrations. The root is like that of anterior teeth, but is more compressed. Maximum size for lateral teeth is 6 mm.

**Remarks:** Two species of this genus are widely reported in the literature, *P. secundus* and *P. tertius*. Teeth of the former species are generally low, with relatively oblique and compressed crowns. Teeth of the latter species are stouter, with slender, weakly sigmoidal crowns. Curiously, the two species are almost always found together. This peculiar distribution pattern has been interpreted as reflecting either the presence of two, ecologically-similar species (Nolf, 1988; Case, 1994), or as sexual dimorphism within a single species (Cappetta, 1987; Kemp et al., 1990). While both possibilities are plausible, the simultaneous occurrence of both forms in the same horizons and the presence of similar sexual dimorphisms in extant carcharhinids support the latter interpretation. Consequently, the name *P. secundus* will be used here, as it has priority.

Case (1994) names a new species, *P. americanus*, from the late Paleocene and early Eocene of Mississippi, based on the small size of the teeth and the presence of an abnormal cusplet on the mesial shoulder. A close examination of the Fisher/Sullivan Bone Bed material suggests that this character is highly variable and present on even some of the largest teeth.

*P. secundus* is known from the late Paleocene through late Eocene of England, Belgium, Morocco, and the Chesapeake Bay region (Cappetta, 1987; Nolf, 1988; Kemp, et al., 1990; Ward and Wiest, 1990; Kent, 1994). The *Physogaleus* figured by Case (1994) from Mississippi (*P. tertius* and, possibly, also *P. americanus*) are considered gender and size variants of *P. secundus*.

#### Other Shark Fossils

Although teeth are by far the most abundant shark fossils in the Fisher/Sullivan Bone Bed, other fossils are also occasionally found. The most frequently collected body fossils are vertebral centra. Shark centra are disks or cylinders of calcified cartilage with concave faces. Each centrum has paired dorsal and ventral cavities that originally

contained projecting cartilaginous processes. Only two general types of centra have been collected from the Fisher/Sullivan Bone Bed. Centra from the lamniform sharks have lateral surfaces with alternating septa and slit-like spaces that are oriented parallel to the central axis (Plate 2.3G). The somewhat simpler centra of the carcharhiniform sharks have smooth lateral surfaces that completely lack the slit-like spaces (Plate 2.3H).

The only other shark body fossils collected from the Fisher/Sullivan Bone Bed are skeletal fragments of calcified cartilage (Plate 2.3I). These fragments appear to be from either the skull or jaws, but are difficult to assign to a more precise position within the skeleton. All of these fragments are relatively dense and have a distinctive structure of closely-spaced prisms.

Shark trace fossils, in the form of fossilized feces, or coprolites, are also commonly collected at the Fisher/Sullivan site. Unlike body fossils, trace fossils do not record actual body parts, but rather materials that have been modified by the activities of sharks. Shark coprolites have a distinctive spiral structure caused by the spiral valve in the intestine (Kent, 1994). In a few examples from this site, coprolites still contain remnants of a meal (Plate 2.3J).

#### DISCUSSION

The uncontaminated nature of the Fisher/Sullivan Bone Bed provides us with a unique window into a paleocommunity from the mid-Atlantic Coastal Plain. Unlike the majority of local fossil beds, which are characterized by extensive reworking and intermixing of different horizons (Kidwell, 1985; Ward, 1984), the Fisher/Sullivan Bone Bed contains a relatively undisturbed community. However, paleoecological interpretations must still be made cautiously. While the Fisher/Sullivan Bone Bed material has not been subjected to the reworking and intermixing typical in most mid-Atlantic coastal plain fossil beds, other sources of contamination are possible.

One shark specimen, in particular, from the Fisher/Sullivan Bone Bed has not been illustrated in the systematic section, since it is almost certainly a contaminant. This tooth is of a Late Cretaceous crow shark, *Squalicorax kaupi* (Agassiz 1843). While this species has been previously recorded from numerous Campanian and Maastrichtian localities worldwide, it has also been found in the Paleocene formations of Missouri and the mid-Atlantic coastal plain (Shourd and Winter, 1980; Lauginiger and Hartstein, 1983; Kent, 1994). In all of these sites, the Paleocene specimens come from horizons that sit unconformably on Late Cretaceous sediments and exhibit evidence of reworking (Shourd and Winter, 1980; personal observations). Consequently, these specimens are likely to have been derived from Late Cretaceous sediments.

The early Eocene *S. kaupi* specimen from the Fisher/Sullivan Bone Bed is more problematical, since there are no adjacent source areas of Late Cretaceous material from

which this tooth could have been reworked. The most likely explanation is that this specimen was a contaminant brought into the site on an improperly cleaned sieve previously used at a Late Cretaceous site in North Carolina (T. Parks, personal communications). The preservation of this specimen is noticeably different from that of most Fisher/Sullivan Bone Bed shark teeth and is consistent with that of the North Carolina site. Further, the absence of additional *S. kaupi* specimens among the tens of thousands of specimens retrieved from the site supports, but does not prove, this explanation.

Despite this one likely contaminant, the Fisher/Sullivan Bone Bed is a surprisingly pure example of an early Eocene paleocommunity. However, it is not an unbiased subsample of the original paleofauna. During fossilization a variety of destructive processes are at work that produce strong biases in the fossil record. In general, several biases are readily apparent in even the best fossil beds. The consequences of these natural biases, in at least general terms, are well-known. First, and most obviously, teeth constitute the vast majority of specimens. The calcified cartilage of the cranial and skeletal elements is less dense than the dentine and enameloid of teeth and is less easily preserved. Consequently, cranial and skeletal fragments are very rare in the Fisher/Sullivan Bone Bed. This disparity is enhanced by the rapid tooth replacement that occurs in many sharks (Maisey, 1984). Second, large individuals are well-represented in the samples, while the smallest individuals are exceedingly rare. This paucity of the smaller teeth within a species is not due to a collecting bias, since the fine-mesh screening techniques used retained all but the most minute (<1 mm) teeth. Instead, it arises from a size-related preservational bias related to the greater susceptibility of smaller teeth to fragmentation, dissolution and hydraulic winnowing. Finally, the species recorded from the Fisher/Sullivan Bone Bed represent only the more common species. Rare species in the original community, particularly those with small teeth, are probably undetectable in the fossil assemblage (Schäfer, 1972; Behrensmeyer and Hill, 1980).

As a consequence of these natural biases in the fossil record, the Fisher/Sullivan Bone Bed paleocommunity is a subset of the species originally present, characterized by the larger and more abundant species. Within single species from the Fisher/Sullivan Bone Bed, the smallest individuals were almost certainly much more abundant in the original community than their depauperate condition as fossils would indicate.

The early Eocene climate of the middle Atlantic coast of eastern North America is generally believed to have been warmer than the present climate (Weems and Grimsley, this volume). The shark paleofauna from the Fisher/Sullivan Bone Bed is consistent with this interpretation. Of the twenty-six shark genera in the Fisher/Sullivan Bone Bed, thirteen (50%) are extant (Table 1). Of these thirteen genera, ten (77%) are well-represented in tropical waters,

twelve (93%) are common in warm temperate waters and only three (23%) are regularly found in cool temperate waters.

Table 1. Climatic preferences for Fisher/Sullivan Bone Bed sharks. The climatic regime where extant genera are most commonly found is indicated with a filled circle (•), while less frequented climatic regimes are indicated with an open circle (°). Probable preferences for extinct genera are indicated with a question mark (?). Climatic preferences for extant genera are from Bigelow and Schroeder, 1948; Castro, 1983; Compagno, 1984; Whitehead, et al., 1984; Smith and Heemstra, 1986; Lythgoe and Lythgoe, 1992; Michael, 1993.

Genus	Warm		Cool
	Tropical	Temperate	Temperate
<i>Hexanchus</i>	•	•	
<i>Echinorhinus</i>	°	•	•
<i>Squalus</i>	°	•	•
<i>Isistius</i>	•	°	
<i>Squatina</i>	•	•	
<i>Heterodontus</i>	•	•	°
<i>Ginglymostoma</i>	•	•	
<i>Nebrius</i>	•	•	
<i>Palaeorhincodon</i>	?	?	
<i>Odontaspis</i>	•	•	
<i>Carcharias</i>	•	•	
<i>Palaeohypotodus</i>	?	?	
<i>Striatolamia</i>	?	?	
<i>Anomotodon</i>	?	?	
<i>Cretolamna</i>	?	?	?
<i>Serratolamna</i>	?	?	?
<i>Otodus</i>	?	?	?
<i>Scyliorhinus</i>	•	•	°
<i>Premontia</i>	?	?	
<i>Galeorhinus</i>	°	•	•
<i>Pachygaleus</i>		?	?
<i>Triakis</i>	•	•	
<i>Palaeogaleus</i>	?	?	
<i>Abdounia</i>	?	?	
<i>Physogaleus</i>	?	?	

Further evidence of the warm water nature of the Fisher/Sullivan Bone Bed shark community is apparent in the affinities of this paleofauna with those from other paleogeographic regions (Table 2). Of the thirty-two shark species in the Fisher/Sullivan Bone Bed, 24 species (75%) also occur in Europe, 16 species (50%) along the Gulf Coast of the United States, and 17 species (53%) in western Africa. Although the Fisher/Sullivan Bone Bed paleofauna has the strongest affinities with the European paleofauna, fifteen of the twenty-four shared species (63%) also occur in at least one of the two warmer water paleofaunas considered.

Table 2. Paleogeographic distribution of Fisher/Sullivan Bone Bed fossil sharks outside of the Atlantic coast of the United States. A filled circle (•) indicates a documented record, while a question mark (?) indicates a doubtful record. References consulted include Leriche (1902, 1905), Casier (1943, 1946, 1967), Arambourg (1952), Thurmond and Jones (1981), Cappetta (1987), Nolf (1988), Kemp, et al. (1990), Ward and Wiest (1990), Case (1994; 1996) and Case, et al. (1996). The central Asian paleofauna of Uzbekistan is strongly allied with European paleofaunas and is included within this paleogeographic region.

Fisher/Sullivan Bone Bed Species	Gulf Coast	Western Europe	Africa	Pacific
<i>Hexanchus</i> sp.		?	•	
<i>Echinorhinus priscus</i>			•	
<i>Squalus crenatidens</i>			•	
<i>Isistius trituratorus</i>		•	•	
<i>Squatina prima</i>		•	•	
<i>Heterodontus lerichei</i>		•		
<i>Ginglymostoma africanum</i>	•		•	
<i>Ginglymostoma subafricanum</i>			•	
<i>Ginglymostoma serra</i>	•			
<i>Nebrius thielensis</i>	•	•		
<i>Palaeorhincodon wardi</i>		•	•	
<i>Orectolobid?</i> sp.				
<i>Odontaspis winkleri</i>		•		
<i>Carcharias hopei</i>	•	•	•	
<i>Carcharias teretidens</i>	•	•		
<i>Palaeohypotodus rutoti</i>		•	?	
<i>Striatolamia macrota</i>	•	•	•	
<i>Anomotodon novus</i>		•		
<i>Cretolamna appendiculata</i>	•	•	•	•
<i>Serratolamna aschersoni</i>	•		•	
<i>Serratolamna lerichei</i>	•	•	•	
<i>Otodus obliquus</i>	•	•	•	?
<i>Scyliorhinus gilberti</i>	•	•		
<i>Premontia degremonti</i>		•		
<i>Galeorhinus ypresiensis</i>	•	•		
<i>Pachygaleus lefevrei</i>	?	•		
<i>Triakis wardi</i>		•		
<i>Palaeogaleus vincenti</i>		•		
<i>Abdounia beaugei</i>	•	•	•	
<i>Abdounia minutissima</i>	•	•	•	
<i>Abdounia recticonia</i>	•	•		
<i>Physogaleus secundus</i>	•	•	•	

Finally, the faunal affinities of the Fisher/Sullivan Bone Bed sharks are not uniformly distributed across all taxonomic orders (Table 3). The squaliforms and squatiniforms are allied with the European and western African faunas, while not sharing any species with the Gulf Coast. The orectolobiforms from the Fisher/Sullivan Bone Bed are primarily warmer-water species also present in the

Gulf Coast and West African faunas. The Fisher/Sullivan Bone Bed lamniforms are markedly cosmopolitan, with five of the ten species found in all three of the other geographic faunas. The carcharhiniforms, while having some shared species with Gulf and African faunas, are predominately European in character.

Table 3. Affinities of the Fisher/Sullivan Bone Bed shark paleofauna to other major paleogeographic areas, listed by taxonomic order. The width of the black bar indicates relative strength of affinity within each order for the Fisher/Sullivan sharks and the sharks of each paleogeographic region.

Taxonomic Order	Gulf Coast	Europe	Western Africa
Hexanchiformes			■
Squaliformes		■	■
Squatiniformes		■	■
Heterodontiformes		■	
Orectolobiformes	■	■	■
Lamniformes	■	■	■
Carcharhiniformes	■	■	■

Based on evidence from the geographic distribution of both extant genera (Table 1) and extinct shark species (Table 2), the Fisher/Sullivan Bone Bed sharks reflect a warm temperate paleofauna that is more strongly influenced by tropical elements than that of the present day Chesapeake Bay area (Wass, 1972). Further, the Fisher/Sullivan Bone Bed sharks show a stronger affinity with contemporaneous eastern Atlantic paleofaunas of Europe and Africa, than with that of the Gulf coast (Table 3).

The Fisher/Sullivan shark paleofauna is also characterized by a predominance of nearshore forms (Table 4) and in this respect is similar to the extant shark fauna of the Chesapeake Bay (Wass, 1972). Based on observations of living sharks (Castro, 1983; Compagno, 1987), species in the genera *Squatina*, *Heterodontus*, *Ginglymostoma*, *Nebrius*, *Odontaspis*, *Carcharias*, *Galeorhinus* and *Triakis* are found predominately in nearshore and inner continental shelf habitats. Less common in the Fisher/Sullivan Bone Bed are deepwater genera, including *Hexanchus*, *Echinorhinus*, *Squalus* and *Scyliorhinus*. Pelagic sharks, such as *Isistius*, are rare.

The remaining extinct genera are more difficult to classify with respect to water depth. The extant genus

*Mitsukurina* is a deepwater form (Compagno, 1984), although the Late Cretaceous mitsukurinid *Scapanorhynchus* is abundant in nearshore fossil beds (Welton and Farish, 1993; Kent, 1994). Consequently, the bathymetric disposition of the Fisher/Sullivan mitsukurinid *Anomotodon* is unclear, although its general rarity in the Fisher/Sullivan Bone Bed is consistent with a deepwater habitat.

Table 4. Habitat preferences for Fisher/Sullivan Bone Bed sharks. The habitats where extant genera are most commonly found are indicated with a filled circle (•), while less frequented habitats are indicated with an open circle (◦). Probable preferences for extinct genera are indicated with a question mark (?). Nearshore sharks are benthic or pelagic species found in the comparatively shallow waters of coastal areas and the inner continental shelf. Offshore sharks are found on the outer continental shelf, continental slope and beyond. Because of the much greater depths involved, offshore species are separated into offshore pelagic (= oceanic) and offshore benthic (= deepwater) habitats. Habitat preferences for extant genera are from Bigelow and Schroeder, 1948; Castro, 1983; Compagno, 1984; Whitehead, et al., 1984; Smith and Heemstra, 1986; Lythgoe and Lythgoe, 1992; Michael, 1993.

Genus	Nearshore	Oceanic	Deepwater
<i>Hexanchus</i>			•
<i>Echinorhinus</i>	◦		•
<i>Squalus</i>	◦		•
<i>Isistius</i>		•	
<i>Squatina</i>	•		◦
<i>Heterodontus</i>	•		
<i>Ginglymostoma</i>	•		
<i>Nebrius</i>	•		
<i>Palaeorhincodon</i>		?	
<i>Odontaspis</i>	•		◦
<i>Carcharias</i>	•		
<i>Palaeohypotodus</i>	?		
<i>Striatolamia</i>	?		
<i>Anomotodon</i>			?
<i>Cretolamna</i>	?		
<i>Serratolamna</i>	?		
<i>Otodus</i>	?	?	
<i>Scyliorhinus</i>	◦		•
<i>Premontia</i>			?
<i>Galeorhinus</i>	•		◦
<i>Pachygaleus</i>	?		
<i>Triakis</i>	•		
<i>Palaeogaleus</i>	?		
<i>Abdounia</i>	?		
<i>Physogaleus</i>	?		

The advanced lamnoid genera (*Cretolamna*, *Serratolamna* and *Otodus*) are widely distributed, but little is known about their preferred habitats. Both *Cretolamna*

and *Serratolamna* are absent from Campanian deepwater sediments in British Columbia (Bill Hessin, unpublished data), even though *Cretolamna* is known from other Pacific localities (Cappetta, 1987). This suggests that *Cretolamna* and *Serratolamna* may have been nearshore sharks, although the evidence is circumstantial at best.

The genus *Otodus* is equally difficult to evaluate. While known from a number of localities in the North Atlantic, there is a record of a single specimen dredged from the deep ocean floor of the Pacific Ocean (see above). As with the later otodontid *Parotodus* (Kent, 1998), this mid-ocean record and general rarity in nearshore sediments imply that *Otodus* may have been more oceanic than many of the other sharks in the Fisher/Sullivan Bone Bed.

The trophic organization of the Fisher/Sullivan shark community is conjectural at present. For extant genera, plausible ecological roles can be readily inferred. But for the extinct genera, conclusions must be much more tentative, and are based on the functional morphology of the teeth and analogies with extant sharks (Castro, 1983; Compagno, 1984; Cappetta, 1987; Kent, 1994).

Based on analogies with living species, the Fisher/Sullivan Bone Bed sharks can be divided into seven trophic guilds. Members of the first, including species in the genera *Squatina*, *Ginglymostoma*, *Nebrius*, *Scyliorhinus* and *Premontia*, have stout clutching teeth and were undoubtedly predators of small, sluggish fishes and bottom-dwelling invertebrates. Included with this trophic guild is the genus *Heterodontus*, which in addition to anterior clutching teeth, has posterior crushing teeth for cracking more heavily armored invertebrates, such as bivalves and gastropods.

A second trophic guild consists of small sharks with comparatively generalized dentitions having tooth crowns that are more oblique and blade-like than the previous group. This group (*Echinorhinus*, *Squalus*, *Galeorhinus*, *Triakis*, *Palaeogaleus*, *Abdounia* and *Physogaleus*) likely fed predominately on small fishes and weakly armored invertebrates, such as squid and shrimp. The first two genera listed were primarily deepwater sharks, while the remaining would have been nearshore sharks.

A third guild, containing the odontaspid and mitsukurinid genera *Odontaspis*, *Carcharias*, *Palaeohypotodus*, *Striatolamia*, and *Anomotodon*, have tall grasping teeth that are adapted for feeding on small active fishes and squid. Weakly armored benthic prey could be consumed by these sharks, but were much less important food sources than for the two previous trophic groups.

The fourth trophic guild contains relatively large sharks with teeth capable of cutting lumps of flesh from large prey. These middle-level predators (*Hexanchus*, *Cretolamna* and *Serratolamna*) were capable of feeding on a range of medium-sized fishes, including sharks in the previous trophic groups. *Hexanchus* differs from the other two genera in this group in being primarily a deepwater form. In modern shark faunas this guild is largely occupied by the

medium to large carcharhinids in the genera *Carcharhinus*, *Galeocerdo* and *Negaprion*. But the Fisher/Sullivan Bone Bed carcharhinids (*Abdounia* and *Physogaleus*) are all comparatively small and belong to the second trophic guild discussed above, where they probably had a life style more like the extant carcharhinid, *Rhizoprionodon*.

Two highly specialized guilds were also represented in the Fisher/Sullivan shark fauna. The cookiecutter sharks (*Isistius*) have a unique life style as parasites of large marine vertebrates and constitute the fifth guild. *Isistius* sharks use their blade-like lower teeth to gouge chunks of flesh from much larger fishes, and in extant species, porpoises and whales. The sixth guild, that of a filter-feeder of small pelagic fishes and invertebrates, contains the archaic whale shark, *Palaeorhincodon*. Both *Isistius* and *Palaeorhincodon* were probably oceanic and only occasionally ventured near the coastline.

The seventh, and final, trophic group is occupied by the giant mackerel shark, *Otodus obliquus*. This shark was fully capable of eating any of the smaller sharks and other vertebrates in the Fisher/Sullivan Bone Bed, although it may have itself been parasitized by *Isistius*. While probably the top carnivore, the exact role of *O. obliquus* in the Fisher-Sullivan paleocommunity is speculative. *O. obliquus* was comparable in size to the extant great white shark, *Carcharodon carcharias*, but it would be unwise to assume that they had identical ecological niches. The biomechanical properties of the teeth of these two species are very different, with *O. obliquus* having crowns that are less likely to fail during dynamic loading and roots that exhibit a higher mechanical advantage for more firmly anchoring teeth to the jaw (Kent, unpublished data). Such teeth are more generalized than the highly specialized cutting teeth of *C. carcharias*, suggesting that *O. obliquus* may have fed on a broader size range of prey and had a more catholic diet than the modern great white.

Overall, the Fisher/Sullivan Bone Bed shark fauna is roughly comparable to the modern mid-Atlantic coastal plain nearshore shark fauna. Many of the genera that are fundamental components of the extant fauna are present at the Fisher-Sullivan site, and probably had similar ecological niches. The only conspicuous difference, as noted above, is in the mid-level, fourth trophic guild. In the Fisher/Sullivan Bone Bed this trophic level is dominated by extinct lamnids (*Cretolamna* and *Serratolamna*), rather than the ubiquitous large carcharhinids of modern faunas. Also, the differences in tooth functional morphology between the top carnivores, *O. obliquus* (Fisher/Sullivan fauna) and *C. carcharias* (modern fauna) probably have some relevance to feeding biology. At present, the scope of these differences is unclear and is the subject of ongoing research.

## BIBLIOGRAPHY

- Arambourg, C. 1952. Les vertébrés fossiles des gisements de phosphates (Maroc-Algérie-Tunisie). *Service Géologique Maroc, Notes et Mémoires*, 92: 1-372.
- Applegate, S. P. 1970. The vertebrate fauna of the Selma Formation in Alabama. Pt. 8, The fishes. *Fieldiana, Geological Memoirs*, 3: 385-433.
- Behrensmeyer, A. K. and A. P. Hill (editors). 1980. *Fossils in the making: vertebrate taphonomy and paleoecology*. University of Chicago Press, Chicago, IL, 338 pp.
- Bigelow, H. B. and W. C. Schroeder. 1948. Sharks. In: *Fishes of the western North Atlantic*. Memoirs of the Sears Foundation for Marine Research, 1 (part 1): 59-579.
- Cappetta, H. 1987. Chondrichthyes II. Mesozoic and Cenozoic Elasmobranchii. *Handbook of Paleichthyology*, vol. 3B. Gustav Fischer Verlag, Stuttgart, 193 pp.
- Cappetta, H. 1992. Carcharhiniformes nouveaux (Chondrichthyes, Neoselachii) de l'Ypresien du Bassin de Paris. *Geobios*, 25: 639-646.
- Carter, J. G., P. E. Gallagher, R. E. Valone and T. J. Rossbach. 1988. Fossil collecting in North Carolina. *Geological Survey Section (North Carolina)*, Bulletin 89, 89 pp.
- Case, G. R. 1978. A new selachian fauna from the Judith River Formation (Campanian) of Montana. *Palaeontographica Abteilung A*, 160: 176-205.
- Case, G. R. 1987. A new selachian fauna from the late Campanian of Wyoming (Teapot Sandstone Member, Mesaverde Formation, Big Horn Basin). *Palaeontographica Abteilung A*, 197: 1-37.
- Case, G. R. 1989. The Upper Cretaceous shark *Cretolamna appendiculata* (Agassiz) in the Raritan Formation (Cenomanian) of New Jersey. *Mosasaurs*, 4: 65-68.
- Case, G. R. 1994. Fossil fish remains from the late Paleocene Tusahoma and early Eocene Bashi Formations of Meridian, Lauderdale County, Mississippi. *Palaeontographica Abteilung A*, 230: 97-138.
- Case, G. R. 1996. A new selachian fauna from the Lower Hornerstown Formation (Early Paleocene/Montian) of Monmouth County, New Jersey. *Palaeontographica Abteilung A*, 242: 1-14.
- Case, G. R., N. I. Udovichenko, L. A. Nesson, A. O. Averianov and P. D. Borodin. 1996. A Middle Eocene selachian fauna from the White Mountain Formation of the Kizylkum Desert, Uzbekistan, C.I.S. *Palaeontographica Abteilung A*, 242: 99-126.
- Casier, E. 1943. Contribution à l'étude des poissons fossiles de la Belgique. III. Quelques espèces nouvelles ou peu connues du Landénien marin. *Bulletin du Musée Royal d'Histoire Naturelle de Belgique*, 19(35): 1-16.
- Casier, E. 1946. La faune ichthyologique de l'Yprésien de la Belgique. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique*, 104: 1-267.
- Casier, E. 1967. Le Landénien de Dormaal (Brabant) et sa faune ichthyologique. *Mémoire Institut Royal des Sciences naturelles de Belgique*, 156: 3-66.
- Castro, J. I. 1983. *The sharks of North American waters*. Texas A & M University Press, College Station, TX, 175 pp.
- Clark, E. and E. Kristof. 1990. Deep-sea elasmobranchs observed from submersibles off Bermuda, Grand Cayman, and Freeport, Bahamas. in: H. L. Pratt, Jr., S. H. Gruber and T. Taniuchi (eds.), *Elasmobranchs as*

living resources: advances in biology, ecology, systematics and the status of the fisheries. *National Oceanic and Atmospheric Administration Technical Report*, no. 90, pp. 269-284.

Compagno, L. J. V. 1984. FAO species catalogue, vol. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Parts 1 & 2. *Food and Agriculture Organization Fisheries Synopsis*, no. 125, 655 pp.

Glückman, L. S. 1958. Rates of evolution in lamnoid sharks. *Doklady Akademii Nauk SSSR*, 123: 568-672.

Glückman, L. S. 1964a. Class Chondrichthyes, subclass Elasmobranchii. in: *Fundamentals of Paleontology*, *Academii Nauk SSSR*, 11: 292-352 (in English translation).

Glückman, L. S. 1964b. *Sharks of the Paleogene and their stratigraphic significance*. Nauka Press, Moscow, Russia, 229 pp.

Glückman, L. S. 1967. Subclass Elasmobranchii (sharks). In: Y. A. Orlov (ed.), *Fundamentals of paleontology, 11, Agnatha, Pisces.*, pp. 292-352.

Hartstein, E. F. and L. E. Decina. 1986. A new Severn Formation (early middle Maastrichtian, Late Cretaceous) locality in Prince Georges County, Maryland. *Mosasaur* 3: 87-96.

Hasegawa, Y. and T. Uyeno. 1967. Fossil fishes. in: K. Tanaka (ed.), *Anancho no Kaseki*. Anancho Educational Committee, pp. 113-117.

Herman, J. 1975. Les sélaciens des terrains néocrétacés et paléocènes de Belgique et des contrées limitrophes. Éléments d'une biostratigraphique intercontinentale. *Mémoires pour Servir à l'Explication Cartes Géologiques et Minières de la Belgique, Service Geologique de Belgique*, 15: 1-450.

International Commission on Zoological Nomenclature. 1987. Opinion 1459. *Carcharias Rafinesque, 1810 (Chondrichthyes, Lamniformes)*: conserved. *Bulletin of Zoological Nomenclature*, 44: 216-217.

Kemp, D. L. Kemp and D. Ward. 1990. *An illustrated guide to the British Middle Eocene vertebrates*. Privately published, London, UK, 59 pp.

Kent, B. W. 1994. *Fossil sharks of the Chesapeake Bay region*. Egan Rees & Boyer, Columbia, MD, 146 pp.

Kent, B. W. 1998. Speculations on the size and morphology of the extinct lamnoid shark, *Parotodus benedeni* (le Hon). *Mosasaur* 6 (in press).

Kidwell, S. M. 1985. Palaeobiological and sedimentological implications of fossil concentrations. *Nature*, 318: 457-460.

Landemaine, O. 1991. Sélaciens nouveaux du crétacé supérieur du sud-ouest de la France quelques apports à la systématique des elasmobranches. *Société Amicale des Géologues Amateurs, Muséum National d'Histoire Naturelle, Paris*, no. 1, 45 pp.

Lauginiger, E. M. and E. F. Hartstein. 1983. *A guide to the fossil sharks, skates and rays from the Chesapeake and Delaware Canal area*. Delaware Geological Survey, Newark, Delaware, Open File Report 21, 64 pp.

Leriche, M. 1902. Les poissons paléocènes de la Belgique. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique*, 22: 1-48.

Leriche, M. 1905. Les poissons tertiaires de la Belgique. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique*, 33: 49-228.

Maisey, J. G. 1984. Higher elasmobranch phylogeny and biostratigraphy. *Zoological Journal of the Linnean Society* 82: 33-54.

Michael, S. W. 1993. *Reef sharks and rays of the world*. Sea Challengers, Monterey, CA, 107 pp.

Nolf, D. 1988. *Fossils de Belgique. Dents de requins et de raies du Tertiaire de la Belgique*. Institut Royal des Sciences naturelles de Belgique, Brussels, Belgium, 184 pp.

Pfeil, F. H. 1983. Zähnmorphologische Untersuchungen an rezenten und fossilen Haien der Ordnungen Chlamydoselachiformes und Echinorhiniformes. *Palaeoichthyologica* 1: 1-315.

Schäfer, W. 1972. *Ecology and palaeoecology of marine environments*. University of Chicago Press, Chicago IL, 568 pp.

Shourd, M. L. and H. F. Winter. 1980. Paleocene megafossils from southeastern Missouri. *Journal of Paleontology* 54: 832-839.

Steel, R. 1985. *Sharks of the world*. Facts on File Publications, New York, NY, 192 pp.

Tessman, N. 1966. Cenozoic sharks of Florida. *Plaster Jacket* 1: 1-7.

Thurmond, J. T. and D. E. Jones. 1981. *Fossil vertebrates of Alabama*. University of Alabama Press, University, Alabama, 244 pp.

Timmerman, J. and R. Chandler. 1995. *Cretaceous and Paleogene fossils of North Carolina*. North Carolina Fossil Club, Durham, NC, 70 pp.

Ward, D. J. 1979. Additions to the fish fauna of the English Palaeogene. 3. A review of the hexanchid sharks with a description of four new species. *Tertiary Research* 2: 111-129.

Ward, D. J. 1989. *Hypotodus verticalis* (Agassiz 1843), *Hypotodus robustus* (Leriche 1921) and *Hypotodus heinzlini* (Casier 1967) Chondrichthyes, Lamniformes, junior synonyms of *Carcharias hopei* (Agassiz 1843). *Tertiary Research* 10: 1-12.

Ward, D. J. and R. L. Wiest, Jr. 1990. A checklist of Palaeocene and Eocene sharks and rays (Chondrichthyes) from the Pamunkey Group, Maryland and Virginia, USA. *Tertiary Research* 12: 81-88.

Wass, M. L. 1972. *A check list of the biota of lower Chesapeake Bay*. Virginia Institute of Marine Science, Special Scientific Report no. 65, Gloucester Point, VA, 290 pp.

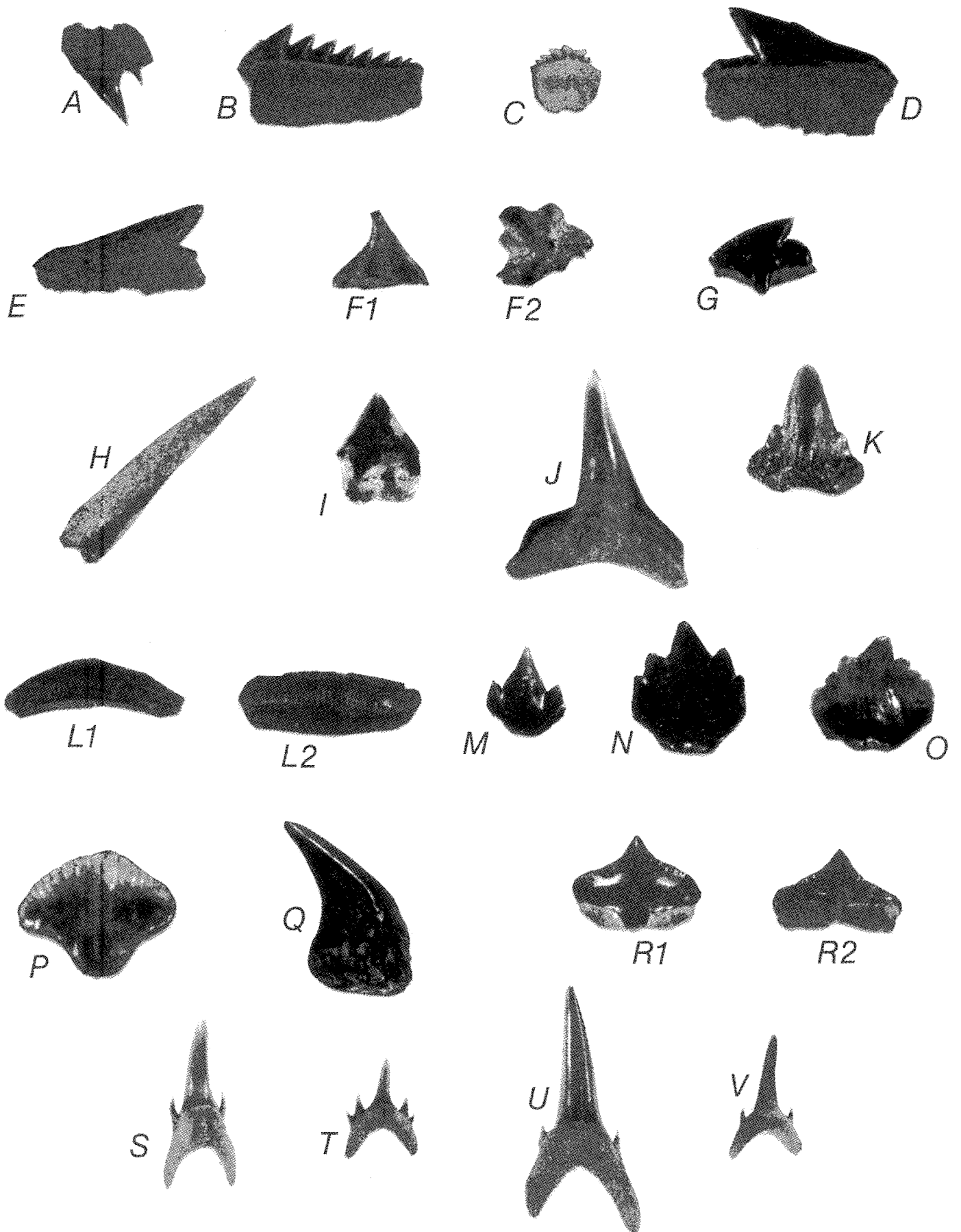
Weems, R. E. 1984. Vertebrate biozones of the Pamunkey Group (Paleocene and Eocene, Maryland and Virginia). in: L. W. Ward and K. Kraft (eds.), *Guidebook for Atlantic Coastal Plain Geological Association 1984 field trip*. Atlantic Coastal Plain Geological Association, pp. 198-203.

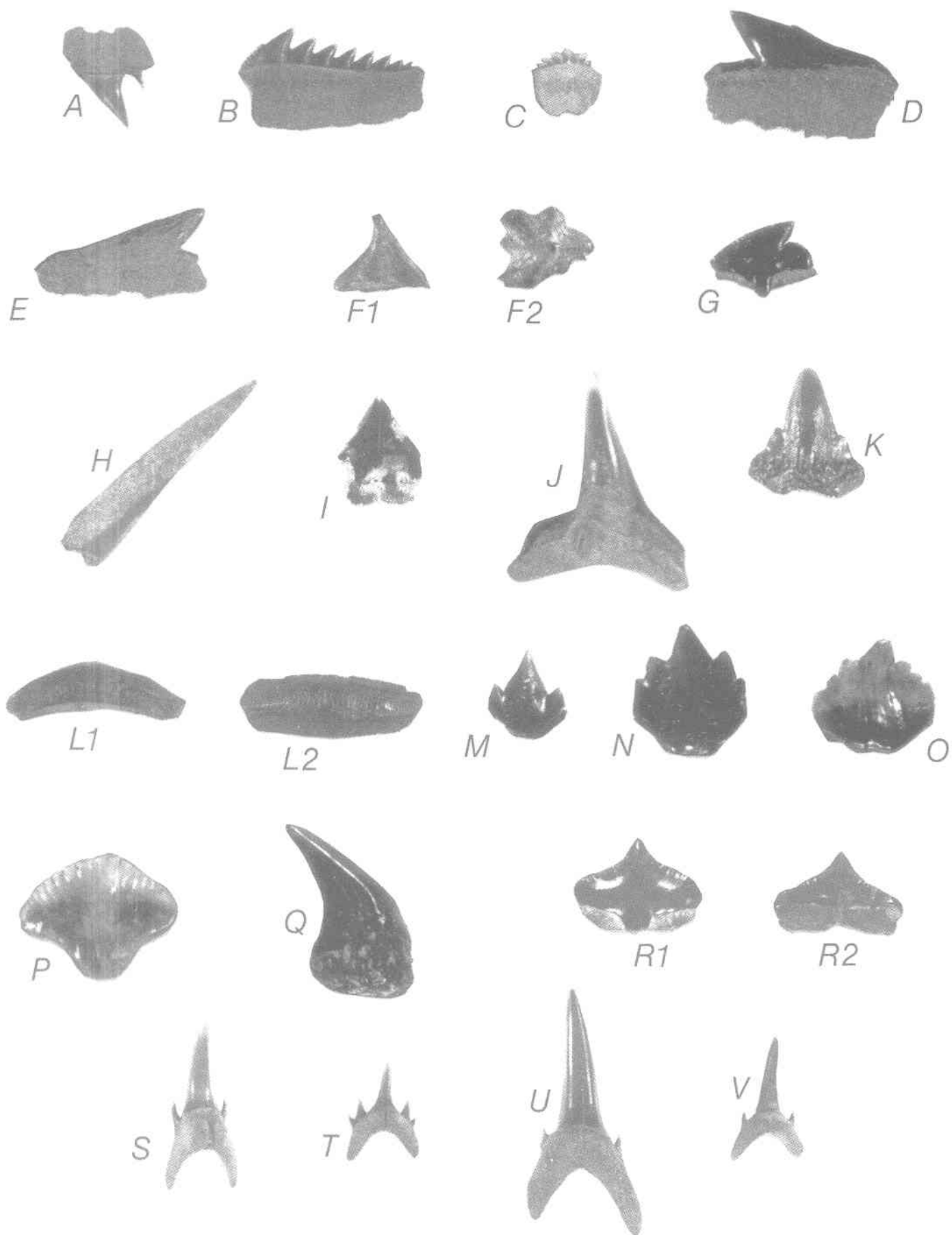
Welton, B. J. and R. F. Farish. 1993. *The collector's guide to fossil sharks and rays from the Cretaceous of Texas*. Before Time, Lewisville, TX, 204 pp.

White, E. I. 1956. The Eocene fishes of Alabama. *Bulletin of American Paleontology*, 36 (no. 156): 122-152.

**Plate 2.1**

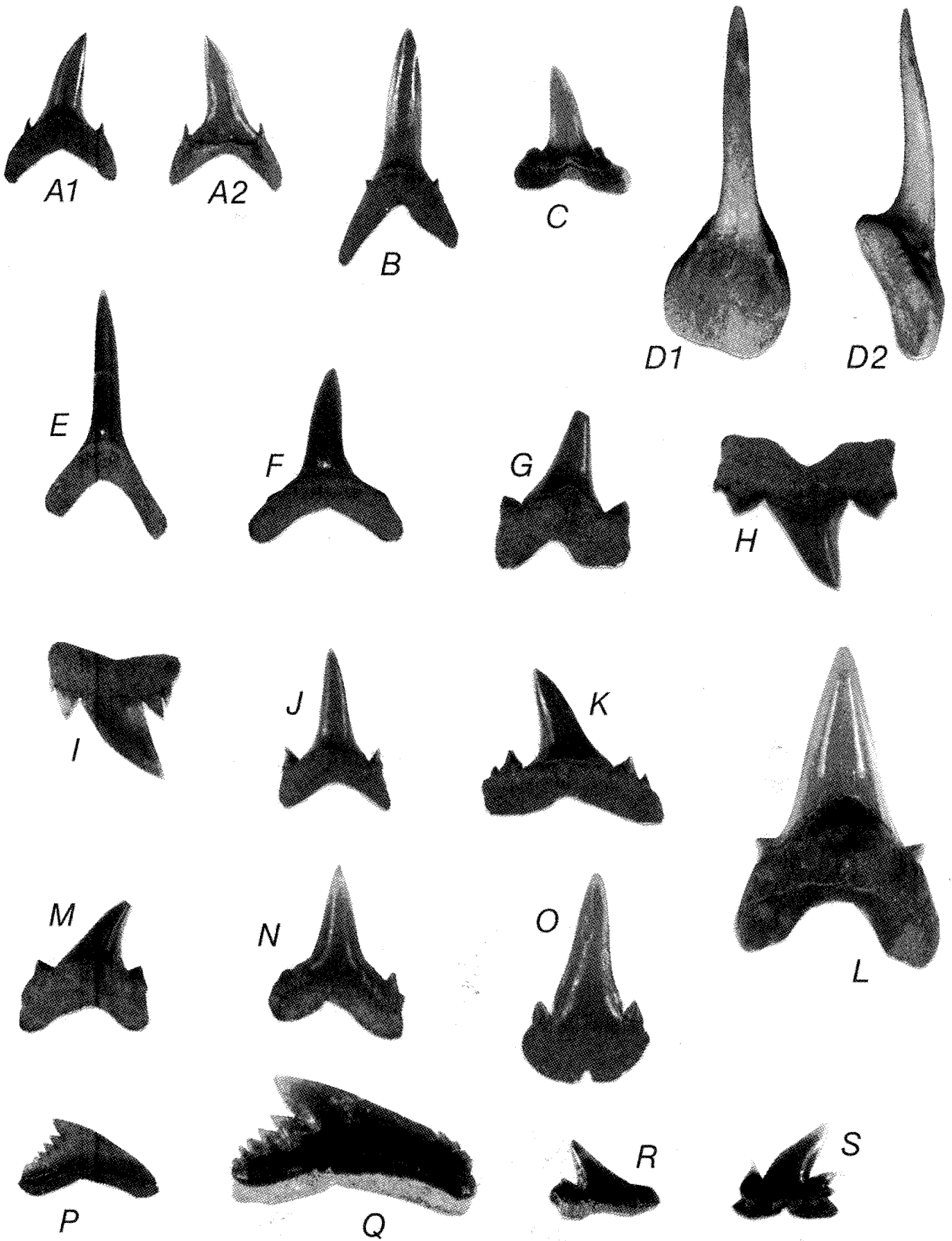
- A - *Hexanchus* sp. upper antero-lateral tooth; lingual view; height = 11 mm (Mike Folmer, USNM 496429).  
B - *Hexanchus* sp. lower antero-lateral tooth; lingual view; width = 18 mm (Mike Folmer, USNM 496430).  
C - *Hexanchus* sp. lower symphyseal tooth; lingual view; width = 14 mm (Mark Bennett collection).  
D - *Echinorhinus priscus* lateral tooth; lingual view; width = 12 mm (Chuck Ball, USNM 496431).  
E - *Echinorhinus priscus* posterior tooth; lingual view; width = 11 mm (Mike Folmer, USNM 496432).  
F - *Echinorhinus priscus* dermal thorn; 1 = lateral view, 2 = apical view; height = 1.7 mm (Mike McCloskey, USNM 496433).  
G - *Squalus crenatidens* lateral tooth; labial view; length = 6 mm (Mike Folmer, USNM 496434).  
H - *Squalid* dorsal fin spine; lateral view; height = 12 mm (Mike McCloskey, USNM 496435).  
I - *Isistius triturator* lower tooth; labial view; height = 6 mm (Chuck Ball, USNM 496436).  
J - *Squatina prima* anterior tooth; lingual view; height = 5 mm (Mike Folmer, USNM 496437).  
K - *Heterodontus lerichei* anterior tooth; labial view; height = 3 mm (Bretton Kent, USNM 496438).  
L - *Heterodontus lerichei* posterior tooth; 1 = labial view, 2 = occlusional view; width = 18 mm (Mike Folmer, USNM 496439).  
M - *Ginglymostoma africanum* tooth; labial view; height = 2 mm (Mike Folmer, USNM 496440).  
N - *Ginglymostoma subafricanum* tooth; labial view; height = 3 mm (Mike McCloskey, USNM 496441).  
O - *Ginglymostoma serra* tooth; labial view; height = 5 mm (Mike Folmer, USNM 496442).  
P - *Nebrius thielensis* tooth; labial view; height = 6 mm (Mike Folmer, USNM 496443).  
Q - *Palaeorhincodon wardi*; profile view; height = 5 mm (Mike Folmer, USNM 496444).  
R - *Orectolobid?* sp. tooth; 1 = labial view, 2 = lingual view; width = 6 mm (Mike Folmer, USNM 496445).  
S - *Odontaspis winkleri* lower anterior tooth; lingual view; height = 16 mm (Mike Folmer, USNM 496446).  
T - *Odontaspis winkleri* lower lateral tooth; lingual view; height = 6 mm (Chuck Ball, USNM 496447).  
U - *Carcharias hopei* lower anterior tooth; lingual view; height = 22 mm (Dick Grier, Jr., USNM 496448).  
V - *Carcharias teretidens* lower anterior tooth; lingual view; height = 12 mm (Bretton Kent, USNM 496449).

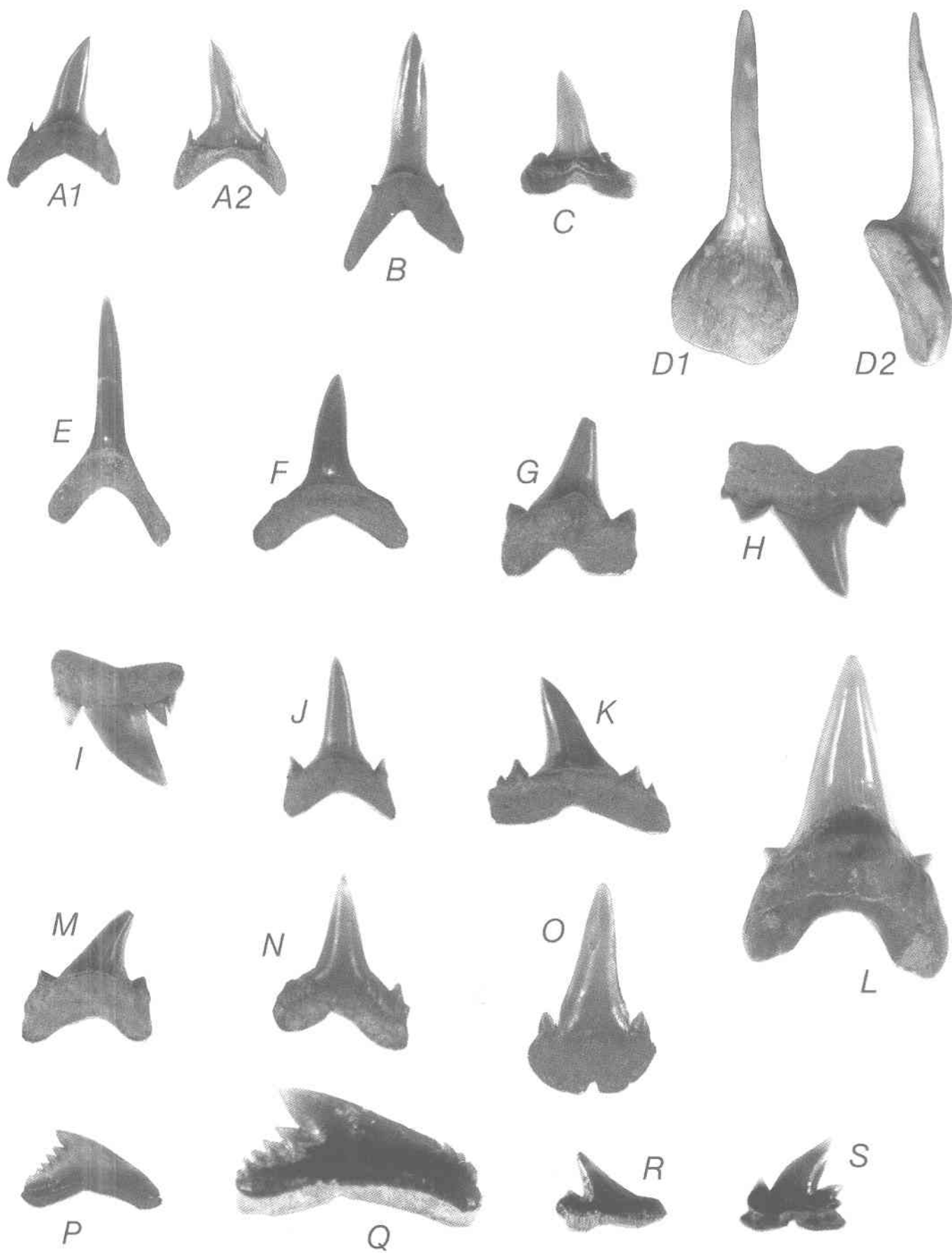




**Plate 2.2**

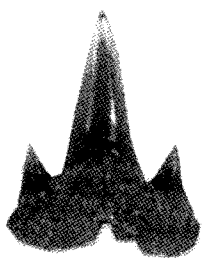
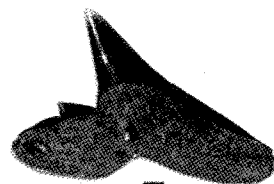
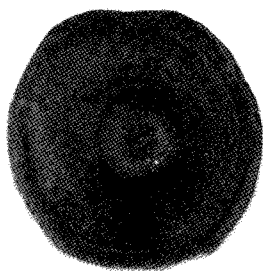
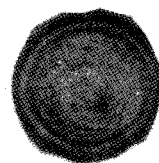
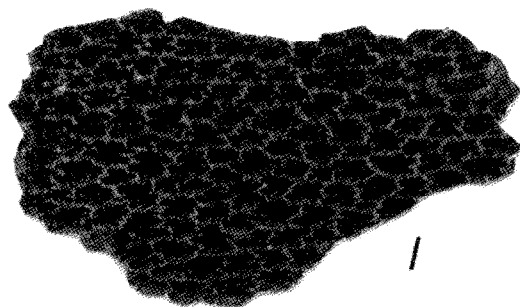
- A - *Palaeohypotodus rutoti* lower anterior tooth; 1 = lingual view, 2 = labial view; height = 28 mm (Mark Bennett, USNM 496450).
- B - *Striatolamia macrota* lower anterior tooth; lingual view; height = 42 mm (Mike Folmer, USNM 496451).
- C - *Striatolamia macrota* lower lateral tooth; labial view; height = 23 mm (Mark Bennett, USNM 496452).
- D - *Striatolamia macrota* pathological anterior tooth; 1 = labial view, 2 = profile view; height = 33 mm (Mike Folmer, USNM 496453).
- E - *Anomotodon novus* lower anterior tooth; lingual view; height = 20 mm (Ron Harding, USNM 496454).
- F - *Anomotodon novus* lower lateral tooth; lingual view; height = 8 mm (Ron Harding, USNM 496455).
- G - *Cretolamna appendiculata* lower anterior tooth; lingual view; height = 15 mm (Mike Folmer, USNM 496456).
- H - *Cretolamna appendiculata* upper lateral tooth; lingual view; height = 14 mm (Mark Bennett collection).
- I - *Serratolamna aschersoni* upper lateral tooth; lingual view; height = 16 mm (Ron Harding, USNM 496457).
- J - *Serratolamna lerichei* lower anterior tooth; lingual view; height = 15 mm (Chuck Ball, USNM 496458).
- K - *Serratolamna lerichei* lower lateral tooth; lingual view; height = 13 mm (Chuck Ball, USNM 496459).
- L - *Otodus obliquus* lower anterior tooth; lingual view; height = 57 mm (Mike Folmer, USNM 496460).
- M - *Otodus obliquus* lateral tooth; lingual view; height = 25 mm (Mike Folmer, USNM 496461).
- N - *Scyliorhinus gilberti* anterior tooth; labial view; height = 1.5 mm (Gary Grimsley, USNM 496494).
- O - *Premontria degremonti* tooth; labial view; height = 4.4 mm (Mike Folmer, USNM 469462).
- P - *Pachygaleus lefevrei* tooth; labial view; width = 10 mm (Ron Harding, USNM 496464).
- Q - *Galeorhinus ypresiensis* tooth; labial view; width = 6 mm (Mike Folmer, USNM 496463).
- R - *Triakis wardi* lateral tooth; labial view; width = 2.6 mm (Dick Grier, Jr. collection).
- S - *Palaeogaleus vincenti* lateral tooth; labial view; height = 2.3 mm (Mark Bennett, USNM 496465).

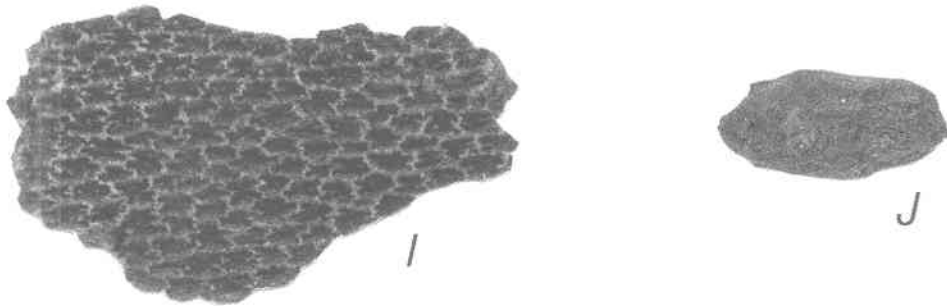
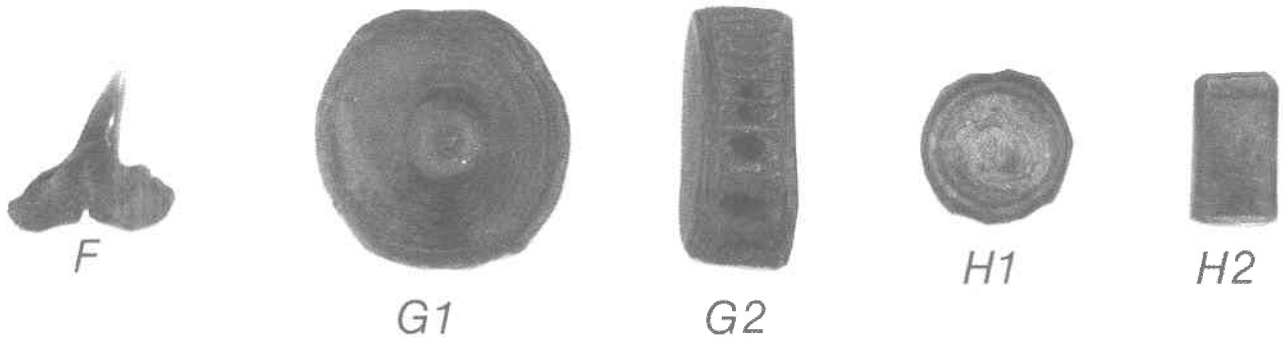
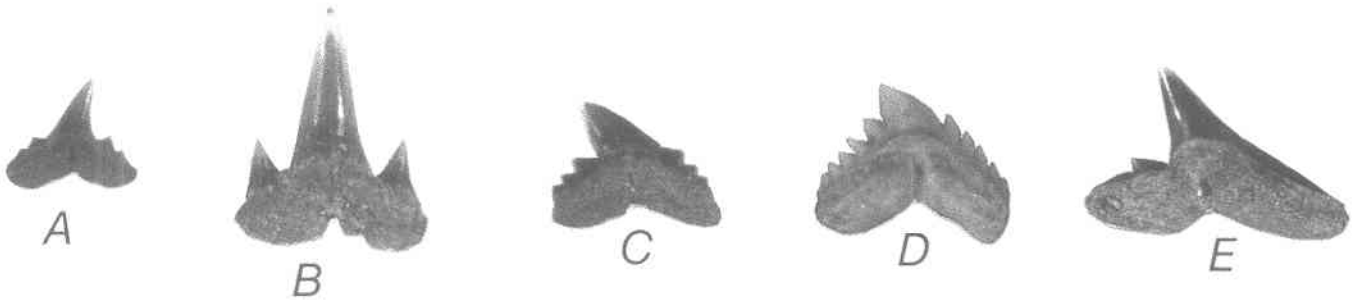




**Plate 2.3**

- A - *Abdounia beaugei* lateral tooth; lingual view; height = 5 mm (Ron Harding, USNM 496466).  
B - *Abdounia minutissima* anterior tooth; lingual view; height = 4.4 mm (Dick Grier, Jr., USNM 496467).  
C - *Abdounia recticona recticona* lateral tooth; lingual view; height = 5.5 mm (Dick Grier, Jr. collection).  
D - *Abdounia recticona claibornensis* lateral tooth; lingual view; height = 5 mm (Chuck Ball collection).  
E - *Physogaleus secundus* female tooth; lingual view; width = 8.6 mm (Gary Grimsley, USNM 496468).  
F - *Physogaleus secundus* male tooth; lingual view; width = 7 mm (Gary Grimsley, USNM 496469).  
G - Lamniform shark vertebral centrum; 1 = axial view, 2 = lateral view; diameter = 16 mm (Gary Grimsley, USNM 496470).  
H - Carcharhiniform shark vertebral centrum; 1 = axial view, 2 = lateral view; diameter = 10 mm (Gary Grimsley, USNM 496471).  
I - Shark cartilage; length = 17 mm (Mike McCloskey, USNM 496472).  
J - Shark coprolite containing fish bones; length = 29 mm (Mike McCloskey, USNM 496473).

*A**B**C**D**E**F**G1**G2**H1**H2**I**J*





## PART 3. RAYS FROM THE FISHER/SULLIVAN SITE

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### INTRODUCTION

The rays (or more properly, the batoids) are a complex group that includes the guitarfishes, sawfishes, skates, electric rays and true rays. In some respects, the rays are the forgotten members of the cartilaginous fishes. While there is an extensive literature devoted to both living and fossil sharks, the rays are much less extensively documented. This bias is due, at least in part, to perceived differences in life style — sharks are large, fast, and dangerous, while the rays are mundane bottom-feeders. Further, many rays also suffer from having small, inconspicuous teeth that can only be collected by labor-intensive screening techniques. But the life style of modern rays, and the difficulty of collecting fossil specimens of many species, should not obscure the reality that this group has a long and exceedingly rich fossil record.

While sharks (Part 2) are the more diverse group of cartilaginous fishes in the Fisher/Sullivan Bone Bed, rays are only slightly less speciose. Eighteen species of rays (Superorder Batomorphii) in two orders and, at least, seven families are known from this site. Although some specimens are large and obvious, many are small and easily overlooked.

In addition to the rays and sharks, there is a third group of cartilaginous fishes commonly found in Cenozoic sediments, the ratfishes or chimaeras. The large durable tooth plates of ratfishes are known from a number of Paleogene sites in the Chesapeake Bay region, but have not been found in the Fisher/Sullivan Bone Bed. Given the relative durability and abundance of these plates, their absence from this site is somewhat puzzling, but may be related to the generally deepwater habits of ratfishes.

**Class Chondrichthyes Huxley 1880**  
**Subclass Elasmobranchii Bonaparte 1838**  
**Cohort Euselachii Hay 1902**  
**Superorder Batomorphii Cappetta 1980**

### Order Rajiformes Berg 1940

The order Rajiformes is highly diverse, containing skates, guitarfishes, sawfishes and electric rays. The body of rajiforms is usually dorsoventrally flattened and frequently has greatly expanded pectoral fins that are contiguous with the head. The eyes and spiracles are located on the dorsal surface of the head, while the mouth and gill slits are on the ventral surface. The tail is long, cylindrical and muscular.

Rajiforms are sluggish, benthic fishes living predominantly over sandy and muddy substrates. The diet is varied, but consists primarily of benthic invertebrates and fishes.

### Family Rhinobatidae Müller and Henle 1838

Guitarfishes (family Rhinobatidae) are elongate, skate-like fishes with a comparatively small, heart-shaped head. The body is stockier than in typical skates and rays, but has the two dorsal fins, paired pelvic fins, and caudal fin that are typical for rajiforms (Figure 3.1; Compagno, 1977).

Guitarfishes are present in nearshore, tropical and warm temperate marine habitats down to depths of about 200 m. The diet consists principally of small mollusks and crustaceans. The maximum body length is about 1.5 m for most species, although one species is known to reach 3 m (Bigelow and Schroeder, 1953; Whitehead, et al., 1984; Smith and Heemstra, 1986; Lythgoe and Lythgoe, 1992).

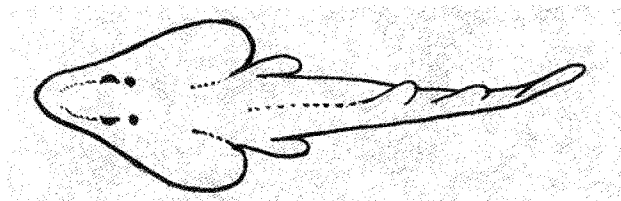


Figure 3.1. Guitarfish.

**Genus *Rhinobatos* Linck 1790**  
***Rhinobatos bruxelliensis* (Jaekel 1894)**

**Figured Specimen:** Plate 3.1A.

**Description:** Teeth of small size, having a comparatively stout crown. The occlusional surface of the crown is convex, and bears a distinct, transverse ridge. The labial face of the crown consists of a heavy, rounded bulge that projects beyond the face of the root. The lingual surface of the crown is prolonged into a tongue-like medial uvula, that is flanked on either side by a shorter, divergent lateral uvula. The enameloid is completely smooth. Maximum size is about 2 mm.

**Remarks:** *R. bruxelliensis* is a widely distributed species, having been previously reported from the early to middle Eocene of Europe (Cappetta, 1987), Mississippi (as *R. sp.*; Case, 1994), and Maryland (Ward and Wiest, 1990). The specimen of *R. bruxelliensis* illustrated here is the first from the Potapaco Member of the Nanjemoy Formation and the first from Virginia.

### Family Pristidae Bonaparte 1838

The family Pristidae (or sawfishes) contains large,

elongate rays, up to 7 m in length, with a compressed, elongated rostrum armed on the lateral margins with large rostral teeth. Rostral teeth differ from oral teeth in two important respects. First, unlike oral teeth, which cease growing before they become functional, rostral teeth grow continuously. Second, while oral teeth are attached to the surface of the jaws, the roots of rostral teeth are housed within deep pits, called alveoli, within the rostrum. The oral teeth of pristids are very small and rarely collected.

Sawfishes have a surprisingly shark-like body (Figure 3.2). However, like other rays, the pectoral fins are attached to the head. As with other rajiforms, the eyes are dorsally-situated, while the mouth and gill slits are on the ventral surface of the head.

Sawfishes are nearshore species in tropical and warm temperate climates. Although principally marine and estuarine, they occasionally stray into freshwater. They are primarily predators of small benthic fishes and invertebrates, but are known to feed occasionally on mid-water fishes, as well. The rostrum is used in feeding, either to probe for fishes or invertebrates buried in soft sediments or to stun swimming fishes (Bigelow and Schroeder, 1953; Whitehead, et al., 1984; Smith and Heemstra, 1986; Lythgoe and Lythgoe, 1992).

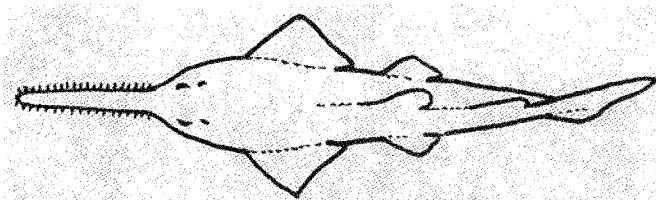


Figure 3.2. Sawfish.

**Genus *Pristis* Linck 1970**  
***Pristis lathamii* Galeotti 1837**

**Figured Specimen:** Plate 3.1B.

**Description:** Very large rostral teeth with tall, compressed crowns of smooth enameloid that are gently curved ventrally. The anterior coronal margin is long and convex and has a broad, rounded cutting edge. The posterior margin is nearly straight to weakly concave and lacks a cutting edge. The surface of the posterior margin is flat with a broad, longitudinal groove running the full height of the crown. The base is broader than the crown and in cross-section has a convex anterior edge and a weakly concave posterior margin. The largest teeth are about 80 mm high, although more typical specimens are about half that size. The oral teeth of *P. lathamii* are not known.

**Remarks:** *P. lathamii* is a widely-distributed species, known from early to late Eocene formations in Belgium, France, Egypt, Morocco, Cabinda, Togo, New Jersey, North Carolina, and from the Woodstock Member of the Nanjemoy Formation and the Piney Point Formation in the

Chesapeake Bay region (Cappetta, 1987; Ward and Wiest, 1990; Timmerman and Chandler, 1995). This is the first record of this species in the Potapaco Member of the Nanjemoy Formation.

*P. lathamii* rostral teeth are at least twice as tall as those of the other three species of sawfishes in the Fisher/Sullivan Bone Bed and have a distinctly concave groove along the posterior margin of the crown that is lacking in the other species.

**Genus *Anoxypristis* White and Moy-Thomas 1941**  
***Anoxypristis mucrodens* (White 1926)**

**Figured Specimen:** Plate 3.1C.

**Description:** Large rostral teeth having a moderately tall, broad and compressed crown covered with smooth enameloid. The coronal margins are tapered and weakly to broadly convex. The crown is roughly elliptical in cross-section, with weakly developed cutting edges, particularly along the posterior margin. The base is conspicuous and generally contiguous with the taper of the coronal margins. Maximum tooth height is about 35 mm.

The oral teeth of *A. mucrodens* are unknown.

**Remarks:** Species in the genus *Anoxypristis* differ from those in the better-known genus *Pristis* primarily on the basis of the internal structure of the rostrum. Since the rostral structure is unknown for this species, and the morphology of the teeth is consistent with that of *Anoxypristis*, it has been allied with that genus (Cappetta, 1987).

*A. mucrodens* has been previously reported from the Eocene of Nigeria and Morocco (White, 1926; Arambourg, 1952).

***Anoxypristis* sp.**

**Figured Specimen:** Plate 3.1D.

**Description:** Small rostral teeth with a crown that is tall, compressed, and covered with smooth enameloid. The coronal margins are tapered and nearly straight. The anterior margin is narrow and moderately sharp, while the posterior margin is broadly rounded. The base is conspicuous and generally contiguous with the taper of the coronal margins. The anterior margin of the base is rounded in cross-section. In many specimens, this margin is not aligned with the coronal margin, but bulges anteriorly when viewed either from above or below. The posterior margin of the base is flat to weakly concave, and appears as a continuation of the posterior coronal margin. The proximal margin of the base is weakly convex. The teeth are small, with a maximum height of about 15 mm. The oral teeth of *Anoxypristis* sp. are unknown.

**Remarks:** This species of sawfish is known from a number of small teeth. As with *A. mucrodens*, the internal structure of the rostrum is unknown. But based on the long,

compressed crown and the absence of a longitudinal groove along the posterior coronal margin, these specimens are provisionally placed in the genus *Anoxypristis*.

These specimens differ from *A. mucrodens* teeth in having nearly straight coronal margins, a relatively sharp anterior cutting edge, and an anterior bulge on the tooth base. However, because of the small size of these specimens, the possibility exists that they represent juvenile teeth of *A. mucrodens*.

**Genus *Propristis* Dames 1883**  
***Propristis schweinfurthi* Dames 1883**

**Figured Specimen:** Plate 3.1E.

**Description:** Large, very broad rostral teeth that lack enameloid on the crown. The coronal apex is broadly pointed. The crown has sharp cutting edges on both the anterior and posterior margins, producing a lenticular cross-section. The anterior cutting edge is straight to weakly convex, except for a shallow concavity immediately apical to the root. The posterior cutting edge is weakly convex. The base has a clearly convex proximal margin. Both the dorsal and ventral surfaces of the base are covered with numerous, incised grooves, parallel to the long axis of the tooth. The largest specimens are about 30 mm high. The oral teeth of *P. schweinfurthi* are unknown.

**Remarks:** *P. schweinfurthi* has rostral teeth that are highly distinctive and unlikely to be confused with those of other Fisher/Sullivan Bone Bed sawfishes. The extreme width of the teeth and the complete absence of enameloid are unmistakable.

*P. schweinfurthi* has been reliably reported from the middle to late Eocene of England, Egypt, Nigeria, Cabinda, Togo and Georgia, and questionably from the Miocene of West Africa (Cappetta, 1987). The specimens of *P. schweinfurthi* from the Fisher/Sullivan Bone Bed are the first reported from the early Eocene and the first from the Chesapeake Bay area.

**Order Myliobatiformes Compagno 1973**

The true rays of the order Myliobatiformes include several very successful families, including the stingrays (Dasyatidae and Urolophidae), the butterfly rays (Gymnuridae), the eagle rays (Myliobatidae), the cownose rays (Rhinopteridae) and the manta rays (Mobulidae). Unlike the rajiform rays discussed above, the myliobatiforms typically have one or more caudal stinging spines for defense (Plate 3.1K). Of the rays in this diverse order, the stingrays and butterfly rays have a primarily benthic lifestyle, while the eagle, cownose, and manta rays are more pelagic. However, with the exception of the manta rays, the myliobatiforms primarily prey on an assortment of bottom-dwelling mollusks and crustaceans (Bigelow and Schroeder, 1953; Whitehead, et al., 1984; Smith and Heemstra, 1986;

Lythgoe and Lythgoe, 1992).

**Family Dasyatidae Jordon 1888**

The stingrays have a highly compressed, rhombohedral body without a dorsal fin or a distinct head (Figure 3.3). The long, whip-like tail is armed with one or more spines that give the group its common name. The dentition consists of either clutching, crushing or grinding teeth, with some species exhibiting a sexual dimorphism in tooth form (Bigelow and Schroeder, 1953; Compagno, 1977).

Stingrays are nearshore species of tropical and warm temperate waters. They are frequently found buried under a thin layer of sediment for camouflage. The diet consists of a variety of small benthic prey that are excavated with the pectoral fins. Although smaller than many other rays, they are known to exceed 2 m (Bigelow and Schroeder, 1953; Whitehead, et al., 1984; Smith and Heemstra, 1986; Lythgoe and Lythgoe, 1992).

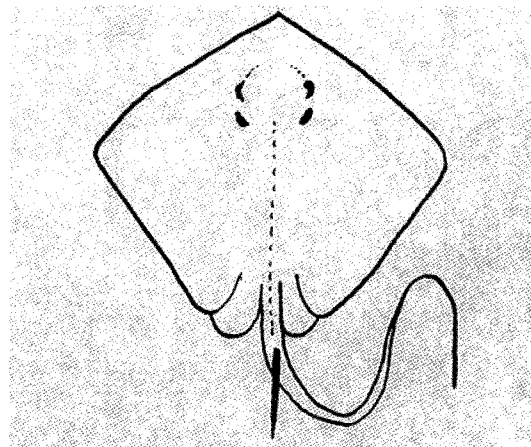


Figure 3.3. Stingray.

**Genus *Hypolophodon* Cappetta 1980**  
***Hypolophodon sylvestris* (White 1931)**

**Figured Specimen:** Plate 3.1F.

**Description:** Small, broadly hexagonal, grinding teeth with a thick crown. The occlusional surface of the crown is weakly convex and smooth, except for a weak transverse crest. The crown is widest at the occlusional surface and tapers slightly toward the narrower basal margin. The lingual face of the crown is irregularly grooved and may have a small, indistinct uvula. The root is relatively broad, but is narrower than the crown. The basal face is flat, with a broad deep nutrient groove that contains several small nutrient pores. The lingual and labial faces of the root have vertical, slit-like nutrient pores. Maximum tooth width is about 7 mm.

**Remarks:** *H. sylvestris* is one of the few dasyatids to have a grinding dentition. As a consequence of using the teeth to feed on thick-shelled shellfish, the transverse crest on the

occlusional face is lacking on most specimens.

Juvenile teeth (which have not been collected from the Fisher/Sullivan Bone Bed) differ from adult teeth in three respects. First, the crown is rhombohedral, rather than hexagonal, in outline. Second, the lingual face of the crown is smooth and has a distinct uvula. Finally, the occlusional surface of the crown is less convex and more nearly flat.

*H. sylvestris* is known from the early Paleocene through early Eocene of Europe, New Jersey and the Chesapeake Bay region (Herman, 1975; Kemp, et al., 1990; Ward and Wiest, 1990; Case, 1996).

**Genus *Meridiania* Case 1994**  
***Meridiania convexa* Case 1994**

**Figured Specimen:** Plate 3.1G.

**Description:** The anterior teeth are small, with a rhomboidal outline in occlusional view. The crown is elevated and strongly convex. The occlusional surface of the crown is covered with numerous sinuous ridges and interspersed pits, which are removed during use, leaving the central portion of the crown as a flattened plateau that exposes the underlying dentine core of the tooth. The lingual face of the crown is prolonged into an abbreviated medial shelf that extends laterally as a distinct ridge. The lingual face of the crown bears a pair of raised, horizontal ridges that converge and join with the labial ridge at the lateral extremities of the tooth. The lingual face has an elliptical, medial depression that is bounded on all sides by an elevated ridge that is contiguous with the horizontal ridges. The root is short and less expansive than the crown. The basal face is flat and has one or two nutrient grooves. Maximum tooth width is about 5 mm.

The lateral teeth are similar to anteriors in overall form, except that the crown is not domed. Instead, the crown has an elevated transverse ridge. In labial view, the transverse ridge has a horizontal apical edge and ends abruptly just medial to the lateral margins of the crown.

**Remarks:** The teeth illustrated here are virtually indistinguishable from the type specimens in Case (1994). Unfortunately, the teeth of many living dasyatid genera are very poorly known (Cappetta, 1987) and the final generic assignment of this species must await a more detailed evaluation of extant genera.

*M. convexa* is only known from the early Eocene of Mississippi, although a second species may also occur in Morocco (Case, 1994).

**Family Gymnuridae Fowler 1934**

The butterfly rays differ from the more familiar stingrays in having a relatively broader, rhombohedral body and a shorter tail (Figure 3.4). The tail may bear a single stinging spine in some species. The dentition consists entirely of clutching

teeth (Bigelow and Schroeder, 1953; Compagno, 1977).

Butterfly rays can be surprisingly large, with the largest individuals measuring 4 m across the pectoral fins. They are primarily nearshore species found to depths of 70 m in warm temperate and tropical seas. The diet consists of a variety of small fishes, crustaceans and mollusks (Bigelow and Schroeder, 1953; Whitehead, et al., 1984; Smith and Heemstra, 1986; Lythgoe and Lythgoe, 1992).

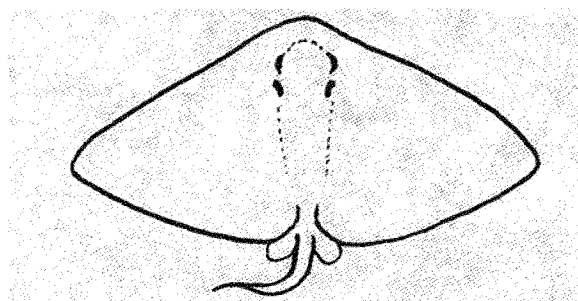


Figure 3.4. Butterfly ray.

**Genus *Jacquhermania* Cappetta 1982**  
***Jacquhermania duponti* (Winkler 1874)**

**Figured Specimen:** Plate 3.1H.

**Description:** Small anterior teeth with a stout, cuspidate crown, covered with smooth enameloid. The transverse ridge is angular, running from the apex of the cusp to the lateral margins on the labial face. The labial face of the crown projects well beyond the root face and has a broad, shallow depression between the branches of the transverse crest. The root is comparatively short, bilobed, and protrudes beyond the crown on the mesial, distal and lingual faces. The basal surface of the root is flattened and has a large, deep nutrient groove that forms a distinct notch on the lingual margin. There is a single nutrient pore within the groove and several lateral pores on the basal face of the root lobes. Maximum tooth size is 2.5 mm.

Lateral teeth are similar to anterior teeth, but are lower, broader and more robust.

**Remarks:** *J. duponti* is the only species within the genus *Jacquhermania*. This species has been previously reported from Europe (Cappetta, 1987; Kemp, et al., 1990). This is the first record of this species from North America.

**Uncertain dasyatoid family**  
**Genus *Coupatezia* Cappetta 1982**  
***Coupatezia woutersi* Cappetta 1982**

**Figured Specimen:** Plate 3.1I.

**Description:** Small teeth with a distinct transverse crest and either a low rounded or weakly cusped crown. The labial face of the crown is ovoid and clearly concave, being bounded on the apical

side by the transverse crest and on the basal side by a transverse ridge. The hollowed labial face is conspicuously ornamented with reticulated wrinkles. The root is tall, with a slender attachment to the crown and a more expansive base. In occlusional aspect, the base projects beyond the crown on the lingual and marginal faces. The basal face of the root is flat, with a deep nutrient groove that forms an obvious notch in the lingual root margin. Nutrient pores are scattered over the basal and labial faces of the root. The largest teeth are about 3 mm wide.

**Remarks:** The teeth of *C. woutersi* exist in two forms — female and lateral male teeth with a broad, low crown, and anterior male teeth with a narrower, sometimes weakly cuspidate, crown (Cappetta, 1982; 1987).

*C. woutersi* is a North Atlantic species, having been previously reported from the middle Eocene of Belgium (Cappetta, 1982), the late Paleocene through middle Eocene of Maryland (Ward and Wiest (1990) and the late Paleocene through early Eocene of Mississippi (Case, 1994), and the middle Eocene of Uzbekistan (Case, et al., 1996).

#### Genus *Heterotorpedo* Ward 1983

#### *Heterotorpedo fowleri* Ward 1983

**Figured Specimen:** Plate 3.1J.

**Description:** Male teeth are small and have a tall crown with a slender cusp and an expanded base. The transverse crest is folded, beginning at the coronal apex as two subparallel ridges extending down the labial face of the cusp and flaring out onto the lateral margins of the expanded coronal base. The base is rectangular, except for a distinctly concave labial margin. The enameloid is generally smooth, although a reticulate transverse ridge, joining the lateral margins of the transverse crest, is typically present on lateral teeth. The root is tall and relatively narrow just basal to the crown, before expanding to form a more globular base. In occlusional view, the enlarged base projects beyond the coronal margins on the lingual and lateral margins. The basal face of the root is flat, and has a large, conspicuous nutrient groove that forms a deep notch in the lingual root margin. Small nutrient pores are scattered over the basal face of the root. Maximum tooth size is about 2 mm tall.

Female teeth have a low, wide crown with an ovoid, weakly concave labial face. The labial face is ornamented with finely reticulate wrinkles and is bounded apically by a well-defined transverse crest and basally by a weak transverse ridge. The root is comparable to that of male teeth, but is more robust in many specimens. Maximum tooth size is about 2 mm.

**Remarks:** In many respects, the male teeth of *H. fowleri* resemble those of *J. duponti*, with a tall, mesio-distally compressed crown and small root. This similarity is particularly pronounced for anterior teeth, where the reticulated transverse ridge typical of more posterior tooth

positions in *H. fowleri* is lacking. The most consistent differences are in the height of the cusp and the shape of the transverse crest. In *J. duponti*, the cusp is moderately elevated and the crest is angular, with comparatively straight cutting edges connecting the coronal apex and lateral margins. This differs from the pattern in *H. fowleri*, where the cusp is noticeably taller and the cutting edges are roughly parallel on the apical half of the crown and diverge rapidly on the basal half. *H. fowleri* is a rare species in the Fisher/Sullivan Bone Bed. At present it is only known from a few male teeth.

*H. fowleri* has been previously reported from the early Paleocene through late Eocene of England, France and Morocco (Cappetta, 1987). The present report is the first record of this species from North America.

### Family Myliobatidae Bonaparte 1838

The eagle rays in the family Myliobatidae are nearshore to semipelagic rays of tropical and warm temperate waters that reach a maximum size of about 2.5 m across the pectoral fins (Figure 3.5). Unlike many rays, they have a distinct head and laterally-placed eyes. The tail is long and whip-like, and bears one or more serrated stinging spines in most species (Plate 3.1K). These spines are dramatically enlarged dermal thorns that occur along the dorsal midline of the body (Plate 3.1L). Eagle rays prey on a variety of shellfish, which they crush with grinding teeth that have been fused into a dental pavement within each jaw (Bigelow and Schroeder, 1953; Whitehead, et al., 1984; Smith and Heemstra, 1986; Lythgoe and Lythgoe, 1992).

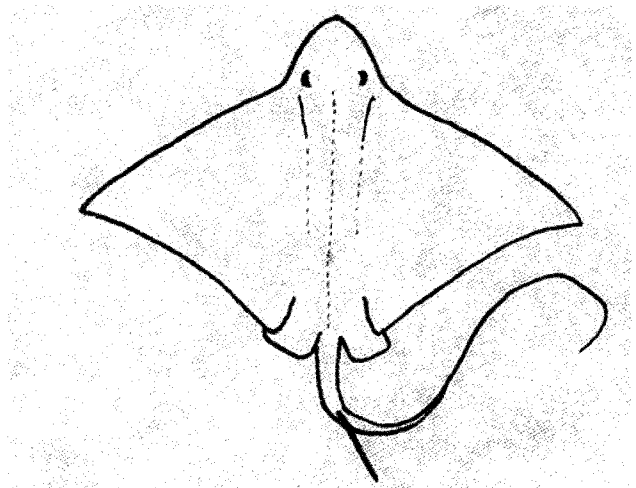


Figure 3.5. Eagle ray.

### Genus *Myliobatis* Cuvier 1817

The jaws of the eagle rays in the genus *Myliobatis* each contain a dental plate consisting of seven rows of fused teeth: a single, broad medial row, flanked on each side by three lateral rows. The upper and lower plates are most easily distinguished from each other by the shape of the

occlusional surface, distinctly convex in upper plates and flat in the lower. Unfortunately, the fused junctions between teeth are relatively weak, and the dental plate is easily dissociated into isolated teeth during fossilization.

There are over 150 named fossil species of *Myliobatis*, most based on minimal material (Cappetta, 1987). Much of this confusion arises because new species frequently have been erected based only on isolated teeth. While the teeth of the broad medial file are the most readily identifiable, subtle differences between the upper and lower plates within a single species can be confusing. Further, the relative width of the medial teeth is size-dependent, being narrowest in the smallest individuals and broadest in the largest (Woodward, 1899).

### ***Myliobatis dixonii* Agassiz 1843**

**Figured Specimen:** Plate 3.1M.

**Description:** The upper medial teeth are large, laterally prolonged hexagons. The labial and lingual margins of these teeth are long and parallel, with a moderately concave labial margin and a corresponding convex lingual margin. The crown is markedly domed medially, becoming thinner at the lateral margins of the tooth. The occlusional surface is smooth in unabraded teeth, although this surface is quickly worn away in most specimens. The labial and lingual surfaces of the crown bear weak wrinkles that interdigitate with those on adjacent teeth. The labial margin of the crown also projects beyond the labial face of the root as a distinct shelf that rests within a matching groove in the lingual face of the tooth. The basal surface of the root is broad and flat, with a large number of deep, longitudinal grooves alternating with thin, parallel lamellae. Maximum tooth width is about 40 mm.

Lower medial teeth are similar to those of the upper jaw but are less broad and have labial and lingual margins that are more weakly arched. The crown is also thinner and not as strikingly domed as that of upper teeth. Maximum tooth width is somewhat smaller than that of upper medial teeth, reaching perhaps 30 to 35 mm. Lateral teeth are considerably smaller than medial teeth and are narrowly hexagonal, with the length equaling or exceeding the width.

**Remarks:** The medial teeth of *M. dixonii* are the narrowest of the three species in the Fisher/Sullivan Bone Bed, having a width in typical specimens that is only about four times that of the length.

*M. dixonii* is a widely-reported species, with records in the early Paleocene through middle Eocene of England, Belgium, Cabinda, Morocco, Mississippi, and the Chesapeake Bay region (Cappetta, 1987; Nolf, 1988; Kemp et al., 1990; Ward and Wiest, 1990; Case, 1994).

### ***Myliobatis striatus* Buckland 1837**

**Figured Specimen:** Plate 3.1N.

**Description:** The upper medial teeth are short, broad

hexagons with angled extremities. The elongated labial and lingual margins of these teeth are parallel. The labial margin is moderately concave, while the matching lingual margin is moderately convex. The crown is weakly domed medially, becoming only slightly thinner at the extremities. The occlusional surface is weakly striated in unworn teeth. The labial and lingual surfaces of the crown are ornamented with delicate vertical wrinkles. A labial coronal shelf and a corresponding lingual groove are present. The basal surface of the root is broad and flat, bearing a large number of alternating deep grooves and lamellae. Maximum tooth width is about 30 mm.

Lower medial teeth resemble upper medials, but are somewhat narrower and less strongly arched. The crown is also thinner and flat to weakly concave. The maximum width is about 30 mm.

Lateral teeth are considerably smaller than medial teeth and are narrow hexagons. The length generally equals or exceeds the width.

**Remarks:** *M. striatus* differs from *M. dixonii* in the relative width of the medial teeth. In *M. dixonii*, the teeth are only moderately broad, having a length that is about 25 percent of the width. The wider teeth of *M. striatus* have a tooth length that is more nearly 15 to 20 percent of tooth width.

Like the previous species, *M. striatus* is widely-distributed, having been found in the early to middle Eocene of England, Tunisia and Nigeria (Cappetta, 1987). Specimens listed as *Myliobatis* sp. that may also be referable to *M. striatus* are known from the middle Eocene of Belgium (Nolf, 1988) and the late Paleocene of Mississippi (Case, 1994).

### ***Myliobatis latidens* Woodward 1888**

**Figured Specimen:** Plate 3.1O.

**Description:** Upper medial teeth are very short and exhibit an extreme lateral expansion. The labial and lingual edges of these teeth are long and very weakly arched to nearly straight. The crown is mildly convex, being only slightly thicker medially than at the lateral margins. The lateral extremities of the medial teeth are angular, although the angles may be rounded in some specimens. The occlusional surface is weakly striate, but is worn in most specimens. The labial and lingual surfaces of the crown have modest vertical wrinkles, along with a horizontal labial shelf and a corresponding lingual groove. The root has a wide, flat basal surface, with numerous deep grooves and thin lamellae. Maximum width is about 30 mm.

Lower medial teeth closely resemble upper medial teeth, but are slightly narrower, with a flat to weakly concave occlusional surface. Maximum size is not precisely known.

Lateral teeth are considerably smaller than medial teeth and are hexagonal to rectilinear. Lateral teeth are relatively narrow, with the length matching or exceeding the width.

**Remarks:** The medial teeth of *M. latidens* are the widest of the three *Myliobatis* species in the Fisher/Sullivan Bone Bed. The width of these teeth is about ten times that of the length.

This is the first record of *M. latidens* from the eastern United States. This species previously has been reported from the middle Eocene of England (Kemp, et al., 1990).

**Genus *Aetobatus* Blainville 1816**  
***Aetobatus irregularis* (Agassiz 1843)**

**Figured Specimen:** Plate 3.1P.

**Description:** The upper dental plate consists of a single row of fused teeth that are short and very broad, with a weakly convex labial face and a subparallel, concave lingual face. The extreme lateral ends of the teeth are slightly narrowed and abruptly curved lingually, overlapping the ends of the next tooth. The crown is relatively thin and has a smooth, flat occlusional surface. The lingual and labial faces of the crown are vertical and weakly ornamented. The root is tall with nearly vertical labial and lingual faces. The broad, flat basal face has alternating grooves and lamellae. The largest teeth are about 80 mm wide.

The lower plate is formed from a single row of broadly arched teeth, with subparallel labial and lingual faces. As on upper teeth, the outermost ends of the lower teeth are slightly narrowed and hooked lingually to overlap the ends of the next tooth in the series. The crown is likewise thin, with a smooth occlusional surface and vertical labial and lingual faces. The root is deep and strongly angled lingually. Both the lingual and comparatively narrow basal faces of the root are covered with tightly-spaced grooves and lamellae. Grooves and lamellae are present on the labial face of the root, but are much more weakly developed. Maximum tooth width is about 80 mm.

**Remarks:** *A. irregularis* is a well-known Atlantic species, having been widely reported from the late Paleocene and early Eocene of Europe and West Africa (Cappetta, 1987; Nolf, 1988; Kemp, et al., 1990), and the early Eocene of the eastern United States (Ward and Wiest, 1990). Ward and Wiest reported this species only from the overlying Woodstock Member of the Nanjemoy Formation, so this is the first record of this species from the Potapaco Member. Teeth of similar overall form, but perhaps from a distinct species, are also known from Alabama (Thurmond and Jones, 1981) and Egypt (Case and Cappetta, 1990).

**Genus *Aetomylaeus* Garman 1908**  
***Aetomylaeus* sp.**

**Figured Specimen:** Plate 3.1Q.

**Description:** Medial teeth in the form of an extended hexagon with the width roughly twice the length. The anterior edge is weakly convex, while the parallel posterior

margin is weakly concave. The occlusional surface is flat and smooth. The labial face of the crown is covered with numerous small pits, while the lingual face has numerous vertical wrinkles. The root is moderately deep and angled lingually. Both the lingual and relatively long basal faces of the root are covered with tightly-spaced grooves and lamellae. Grooves and laminae are present on the labial face of the root, but are much more weakly developed. Maximum tooth width of about 20 mm.

**Remarks:** This species is known from several medial teeth that are unusual in that they have the extended hexagonal crown typically found in *Rhinoptera* and *Myliobatis*, but an angled root strongly resembling that of *Aetobatus*. In some respects, this tooth resembles the anterior embryonic teeth of *Aetobatus* (Bigelow and Schroeder, 1953), but is at least an order of magnitude too large.

This highly distinctive tooth is tentatively allied to the myliobatid genus *Aetomylaeus*. Unfortunately, this genus is very poorly known in the fossil state, having been reported only from the Pliocene, and possibly Miocene, of France (Cappetta, 1987). Recent species in this genus have medial teeth that are four to six times broader than they are long (Garman, 1913), rather than the two-fold difference observed in the specimens from the Fisher/Sullivan Bone Bed.

**Family Rhinopteridae Jordan & Evermann 1896**  
**Genus *Rhinoptera* Cuvier 1829**

The cownose rays (family Rhinopteridae) are closely allied to the eagle rays (family Myliobatidae). Like the eagle rays, cownose rays are nearshore to semipelagic species in tropical and warm temperate oceans. Also like the eagle rays, they have a distinct head and laterally-placed eyes. The tail is longer than the body and usually has one or more serrated stinging spines (Figure 3.6). Cownose rays have seven or more rows of grinding teeth that are fused into a dental pavement and used to crush shellfish and benthic finfishes. Maximum size is in excess of 2 m (Bigelow and Schroeder, 1953; Ursin, 1977; Whitehead, et al., 1984; Smith and Heemstra, 1986).

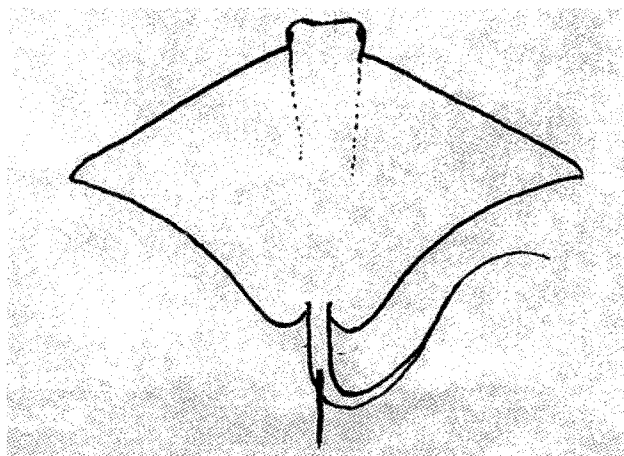


Figure 3.6. Cownose ray.

***Rhinoptera sherboni* White 1926a****Figured Specimen:** Plate 3.1R.

**Description:** The medial teeth are large, slightly prolonged hexagons. The labial and lingual margins of these teeth are moderately long and parallel, with straight labial and lingual margins. The occlusional surface of the crown is flat and smooth, although it may be pitted in worn teeth. The labial and lingual surfaces of the crown bear complex wrinkles that interdigitate with those on adjacent teeth. The labial margin of the crown forms a conspicuous shelf that fits within a corresponding groove on the lingual face. The basal surface of the root is broad and very flat, with a large number of deeply incised, longitudinal grooves. Maximum tooth width is about 10 mm.

Lateral teeth immediately adjacent to the medial teeth are only slightly smaller than medial teeth. Unlike medial teeth, they may be slightly asymmetrical. More distally placed lateral teeth are not prolonged and closely resemble the lateral teeth of *Myliobatis*.

**Remarks:** While dental plates of *Rhinoptera* are easily identified by the similar morphologies of medial and adjacent lateral teeth, isolated teeth are more difficult to recognize. Specimens of *R. sherboni* are easily mistaken for medial teeth of *M. dixonii*, being only slightly narrower than those of the latter species.

*Rhinoptera* is represented only by a few isolated teeth from the Fisher/Sullivan Bone Bed. Therefore, in the absence of articulated dental plates, their assignment to *R. sherboni* must be considered tentative. *R. sherboni* has been previously reported from the middle Eocene of Africa and England (Cappetta, 1987; Kemp, et al., 1990).

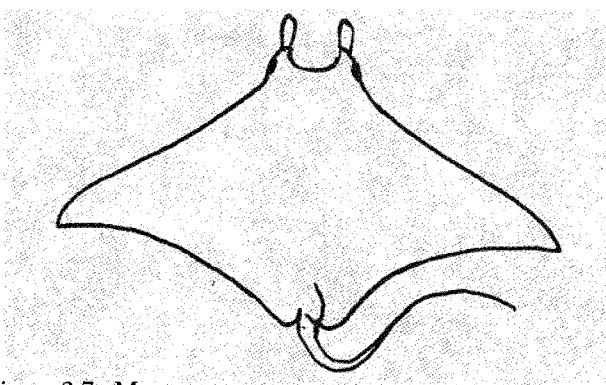


Figure 3.7. Manta ray.

**Family Mobulidae Gill 1893**

The manta rays in the family Mobulidae are huge rays that can be up to 9 m across the pectoral fins. Although predominately pelagic, they do venture near shore on occasion. As with many other rays, they are warm temperate or tropical species. The body is rhombohedral, with a whip-like tail that generally lacks stinging

spines. The most distinctive feature of the mantas is a pair of large, flap-like cephalic fins that are used to direct water into the mouth (Figure 3.7). Manta rays are filter-feeders that strain planktonic invertebrates and small fishes from the water with their gills (Bigelow and Schroeder, 1953; Whitehead, et al., 1984; Smith and Heemstra, 1986; Lythgoe and Lythgoe, 1992).

**Genus *Archaeomanta* Herman 1979a*****Archaeomanta melenhorsti* Herman 1979a****Figured Specimen:** Plate 3.1S.

**Description:** Small teeth with a tall, mesio-distally compressed crown that is strongly bent lingually. The base of the crown is ovate in cross-section and may angle labially in some specimens before abruptly curving lingually. The curved apex is mesio-distally compressed and has a cutting edge on the labial margin. The root is very short and globular. In basal view, the root is heart-shaped with a deep nutrient groove that forms a conspicuous notch in the lingual margin. The surface of the root may be smooth or irregularly ruffled. Maximum tooth height is about 3.5 mm.

**Remarks:** The teeth of *A. melenhorsti* are not easily confused with other teeth from the Fisher/Sullivan Bone Bed. The strongly arched, mesio-distally compressed crown and short, abbreviated root are distinctive.

*A. melenhorsti* has been recorded from the late Paleocene to middle Eocene of England, Belgium, Morocco, Mississippi and Uzbekistan (Cappetta, 1987; Kemp, et al., 1990; Case, 1994; Case, et al., 1996).

**Genus *Burnhamia* Cappetta 1976*****Burnhamia daviesi* (Woodward 1889d)****Figured Specimen:** Plate 3.1T.

**Description:** Broadly hexagonal teeth with a comparatively smooth, markedly concave occlusional surface. The hollowed occlusional surface is surrounded by a distinct marginal ridge. The labial and lingual faces of the crown are both steeply sloping. The relatively low labial face projects well beyond the labial face of the root as a conspicuous shelf. Lingual face of the crown does not extend past the lingual face of the root, and is noticeably more elevated than the labial face of the crown. The lingual face of the crown has multiple uvulae, each corresponding to a nutrient groove in the root. The root is tall, with a flat basal face. The basal root face is traversed by a number of deep, longitudinal grooves, each of which usually contains a single nutrient pore. Width of largest teeth is about 20 mm.

**Remarks:** The dentition of *B. daviesi* consists of multiple files of teeth that are broadest along the midline of the jaw and become progressively narrower laterally (Cappetta, 1987).

*B. daviesi* is an Atlantic species, having been reported from the

late Paleocene through middle Eocene of England, Belgium, Uzbekistan, Morocco, Mississippi and the Chesapeake Bay area (Cappetta, 1987; Nolf, 1988; Kemp, et al., 1990; Ward and Wiest, 1990; Case, 1994; Case, et al., 1996).

## DISCUSSION

The uncontaminated nature of the Fisher/Sullivan Bone Bed provides a rare opportunity to examine a largely intact ray paleocommunity. However, as discussed with respect to the fossil sharks from this site (Kent, this volume), the ray paleofauna of the Fisher/Sullivan Bone Bed is inherently biased against both the rarest species and individuals with the smallest teeth. Despite these biases, a number of interesting patterns arise from an evaluation of the Fisher/Sullivan Bone Bed rays.

The Fisher/Sullivan ray paleofauna is consistent with the warmer climatic conditions believed to have prevailed along the eastern coast of North America during the early Eocene (Weems and Grimsley, this volume). All of the extant ray genera in the Fisher/Sullivan Bone Bed (*Rhinobatos*, *Pristis*, *Anoxypristis*, *Myliobatis*, *Aetobatus*, *Aetomylaeus* and *Rhinoptera*) are warm temperate or tropical forms, with no marked affinity for cool temperate climates (Table 1). Although no extant dasyatoid or mobulid genera are present in the Fisher/Sullivan Bone Bed, living members of these groups are tropical to warm temperate in distribution. This suggests that the extinct Fisher/Sullivan Bone Bed dasyatoids (*Hypolophodon*, *Meridania*, *Jacquhermania*, *Coupatezia* and *Heterotorpedo*) and mobulids (*Archaeomanta* and *Burnhamia*) probably had similar distributions (Table 1).

Table 1. Climatic preferences for Fisher/Sullivan Bone Bed rays. The climatic regime where extant genera are most commonly found is indicated with a filled circle (•). Probable preferences for extinct genera are indicated with a question mark (?). Climatic preferences for extant genera are from Bigelow and Schroeder, 1953; Whitehead, et al., 1984; Smith and Heemstra, 1986; Lythgoe and Lythgoe, 1992; and Michael, 1993.

Genus	Tropical	Warm Temperate	Cool Temperate
<i>Rhinobatos</i>	•	•	
<i>Pristis</i>	•	•	
<i>Anoxypristis</i>	•	•	
<i>Propristis</i>	?	?	
<i>Hypolophodon</i>	?	?	
<i>Meridania</i>	?	?	
<i>Jacquhermania</i>	?	?	
<i>Coupatezia</i>	?	?	
<i>Heterotorpedo</i>	?	?	
<i>Myliobatis</i>	•	•	
<i>Aetobatus</i>	•	•	
<i>Aetomylaeus</i>	•	•	
<i>Rhinoptera</i>	•	•	
<i>Archaeomanta</i>	?	?	
<i>Burnhamia</i>	?	?	

The Fisher/Sullivan rays exhibit a clear affinity to European ray paleofaunas, with a substantial intermixing of more tropical forms found in the Gulf Coast and west African paleofaunas (Table 2). Of the eighteen species in the Fisher/Sullivan Bone Bed, fourteen (78%) are known from European paleofaunas, ten (56%) are found in west African paleofaunas and seven (39%) occur in Gulf Coast paleofaunas. However, of the fourteen Fisher/Sullivan Bone Bed species known from the European paleofauna, eleven (79%) also occur in at least one of the warmer water paleofaunas examined. This suggests that both the European and Fisher/Sullivan ray paleofaunas were probably warm temperate communities with a pronounced tropical influence.

As with the sharks, there are some differences in the affinities of individual taxonomic orders, although the differences are not quite as striking (Table 3). The Rajiformes have equally strong affinities with both the European and West African paleofaunas. The more diverse Myliobatiformes have a noticeable similarity with the European paleofauna, although seven of the ten shared species are also recorded from one of the warmer water paleofaunas as well.

Table 2. Paleogeographic distribution of Fisher/Sullivan Bone Bed fossil rays outside of the Atlantic coast of the United States. A filled circle (•) indicates a documented record, while a question mark (?) indicates a doubtful record. References consulted include Leriche (1902, 1905), Casier (1943, 1946, 1967), Arambourg (1952), Thurmond and Jones (1981), Cappetta (1987), Nolf (1988), Kemp, et al. (1990), Ward and Wiest (1990), Case (1994) and Case, et al. (1996). The central Asian paleofauna of Uzbekistan is strongly allied with European paleofaunas and is included within this paleogeographic region.

Fisher/Sullivan Bone Bed Species	Gulf Coast	Europe	Western Africa	Pacific
<i>Rhinobatos bruxellensis</i>	•	•		
<i>Pristis lathamii</i>		•	•	
<i>Anoxypristis mucrodens</i>			•	
<i>Anoxypristis</i> sp.				
<i>Propristis schweinfurthi</i>		•	•	
<i>Hypolophodon sylvestris</i>		•		
<i>Meridania convexa</i>	•			
<i>Jacquhermania duponti</i>		•		
<i>Coupatezia woutersi</i>	•	•		
<i>Heterotorpedo fowleri</i>		•	•	
<i>Myliobatis dixonii</i>	•	•	•	
<i>Myliobatis striatus</i>	?	•	•	
<i>Myliobatis latidens</i>		•		
<i>Aetobatus irregularis</i>	•	•	•	
<i>Aetomylaeus</i> sp.				
<i>Rhinoptera sherboni</i>		•	•	
<i>Archaeomanta melenhorsti</i>	•	•	•	
<i>Burnhamia daviesi</i>	•	•	•	

Table 3. Affinities of the Fisher/Sullivan Bone Bed ray paleofauna with other major paleogeographic areas, listed by taxonomic order. The width of the black bar indicates the relative strength of affinity within an order for the Fisher/Sullivan rays and the rays of each paleogeographic region.

Taxonomic Order	Western		
	Gulf Coast	Europe	Africa
Rajiformes	■	■	■
Myliobatiformes	■	■	■

The Fisher/Sullivan Bone Bed ray fauna is also dominated by nearshore genera (Table 4). With the probable exception of *Archaeomanta* and *Burnhamia*, all of the other genera in the Fisher/Sullivan Bone Bed are known, or inferred, to have lived primarily in coastal and inner shelf habitats. Some genera, such as *Myliobatis* and *Aetobatus*, occasionally venture out onto the outer continental shelf, but are still principally denizens of the inner shelf.

Table 4. Habitat preferences for Fisher/Sullivan Bone Bed rays. Preferred habitats of extant genera are indicated with a filled circle (•), while habitats where extant genera are only occasionally found are indicated with an open circle (◦). Probable preferences for extinct genera are indicated with a question mark (?). Nearshore rays are benthic or pelagic species found in the comparatively shallow waters of coastal areas and the inner continental shelf. Offshore rays are found on the outer continental shelf, continental slope and beyond. Because of the much greater depths involved, offshore species are separated into offshore pelagic (= oceanic) and offshore benthic (= deepwater) habitats. Habitat preferences for extant genera are from Bigelow and Schroeder, 1953; Whitehead, et al., 1984; Smith and Heemstra, 1986; Lythgoe and Lythgoe, 1992; Michael, 1993.

Genus	Nearshore	Oceanic	Deepwater
<i>Rhinobatos</i>	•		
<i>Pristis</i>	•		
<i>Anoxypristis</i>	•		
<i>Propristis</i>	?		
<i>Hypolophodon</i>	?		
<i>Meridania</i>	?		
<i>Jacquhermania</i>	?		
<i>Coupatezia</i>	?		
<i>Heterotorpedo</i>	?		
<i>Myliobatis</i>	•	◦	
<i>Aetobatus</i>	•	◦	
<i>Aetomylaeus</i>	•	◦	
<i>Rhinoptera</i>	•	◦	
<i>Archaeomanta</i>		?	
<i>Burnhamia</i>		?	

The Fisher/Sullivan Bone Bed rays are members of four distinct ecological guilds. The most widely represented is composed of benthic rays that feed almost exclusively on benthic shellfish. Only one extant genus in the Fisher/Sullivan Bone Bed (*Rhinobatos*) belongs to this guild, but based on analogies with extant forms, five extinct dasyatoid genera (*Hypolophodon*, *Meridania*, *Jacquhermania*, *Coupatezia*, and *Heterotorpedo*) should also be included. Two of these genera (*Coupatezia* and *Heterotorpedo*) have sexually dimorphic teeth. Comparisons with extant dasyatoids suggest that females had relatively low, domed teeth, while males had more elevated, cuspidate teeth (Cappetta, 1987; Nishida and Nakaya, 1990). The more elevated teeth of males may mean that they preyed more extensively on weakly armored shellfish, such as shrimp, or small benthic fishes, than did females. Among members of this guild in the Fisher/Sullivan Bone Bed, the genus *Hypolophodon* is unique in having grinding teeth. These teeth would have permitted this ray to feed on more heavily armored shellfish than other members of the guild.

The second guild contains benthic generalists. Members of this group consumed benthic shellfishes and finfishes, but were also capable of feeding on nearshore pelagic fishes, as well. This guild is dominated by the sawfishes in *Pristis*, *Anoxypristis*, and probably *Propristis*. The rostrum in these rays is highly versatile, and can be used either to probe for buried prey or stun swimming fishes. Males of some genera in the first guild may have paralleled the habits of the sawfishes, but were probably poorly adapted for feeding on pelagic fishes.

The third guild consists of nearshore pelagic rays that fed on benthic shellfishes. Myliobatids (*Myliobatis*, *Aetobatus*, *Aetomylaeus*, and *Rhinoptera*) are all members of this guild. The dental plates of fused grinding teeth are highly efficient at crushing heavily armored shellfish, such as crabs, clams, and snails.

The final guild, the oceanic filter-feeders, contained the mobulid genera *Archaeomanta* and *Burnhamia*. The mantas are a highly distinctive group of rays, because of the prominent cephalic fins that help funnel water into the mouth. Small planktonic invertebrates and fishes were filtered from the water by the gills and then swallowed. Cappetta (1976) noted that the teeth of *Burnhamia* consistently show relatively little wear, suggesting a diet of small or soft-bodied prey. Such prey could include salps, jellyfishes and other soft-bodied, pelagic invertebrates.

Interestingly, the Fisher/Sullivan Bone Bed lacks one group of rays, the skates (Rajiformes, Rajidae), that would be expected based on the extant ichthyofauna of the Chesapeake Bay. The extant fauna has four species of skates, with at least one species, the clearnose skate (*Raja eglanteria*), being particularly abundant (Wass, 1972). Although the rajids arose in the Cenomanian, and the extant genus *Raja* appeared by the early Eocene (Ward, 1984; Cappetta, 1987), no specimens have been found in the Fisher/Sullivan Bone Bed. This absence of fossil skates at the Fisher/Sullivan site is puzzling, but not particularly troubling. Of the seven skate species living

along the mid-Atlantic coast today, five (71%) have ranges that extend from roughly Cape Hatteras, North Carolina northward into the colder waters of the North Atlantic, while only two (29%) have ranges that extend appreciably southward into the warmer waters off the southeastern coastline of the United States (Ursin, 1977). This predominately cool temperate distribution of skates is consistent with global patterns of rajid distribution, where skates are most abundant in the nearshore waters of high latitudes or in the deep sea at lower latitudes (Whitehead, et al., 1984; Smith and Heemstra, 1986). Consequently, the warm temperate climate that prevailed along the mid-Atlantic coast during the early Eocene may have been only marginally suitable for skates.

### BIBLIOGRAPHY

- Arambourg, C. 1952. Les vertébrés fossiles des gisements de phosphates (Maroc-Algérie-Tunisie). *Service Géologique Maroc, Notes et Mémoires*, 92: 1-372.
- Bigelow, H. B. and W. C. Schroeder. 1953. Sawfishes, guitarfishes, skates and rays, and chimaeroids. In: *Fishes of the western North Atlantic*, Memoir of the Sears Foundation for Marine Research, 1 (part 2): 1-588.
- Cappetta, H. 1976. Sélaciens nouveaux du London Clay de l'Essex (Yprésien du Bassin de Londres). *Géobios*, 9: 551-574.
- Cappetta, H. 1982. Révision de *Cestracion duponti* Winkler 1874 (Selachii, Batomorphii) du Bruxellien de Woluwe-Saint-Lambert (Eocène moyen de Belgique). *Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie*, 19: 113-125.
- Cappetta, H. 1987. Chondrichthyes II. Mesozoic and Cenozoic Elasmobranchii. *Handbook of Paleoichthyology*, vol. 3B. Gustav Fischer Verlag, Stuttgart, 193 pp.
- Case, G. R. 1994. Fossil fish remains from the late Paleocene Tuscahoma and Eocene Bashi Formations of Meridian, Lauderdale County, Mississippi. *Palaeontographica Abteilung A*, 230: 97-138.
- Case, G. R. 1996. A new selachian fauna from the Lower Hornerstown Formation (early Paleocene/Montian) of Monmouth County, New Jersey. *Palaeontographica Abteilung A*, 242: 1-14.
- Case, G. R. and H. Cappetta. 1990. The Eocene selachian fauna from the Fayum Depression in Egypt. *Palaeontographica Abteilung A*, 212: 1-39.
- Case, G. R., N. I. Udovichenko, L. A. Nessov, A. O. Averianov and P. D. Borodin. 1996. A middle Eocene selachian fauna from the White Mountain Formation of the Kizylkum Desert, Uzbekistan, C.I.S. *Palaeontographica Abteilung A*, 242: 99-126.
- Casier, E. 1943. Contribution à l'étude des poissons fossiles de la Belgique. III. Quelques espèces nouvelles ou peu connues du Landénien marin. *Bulletin du Musée Royal d'Histoire Naturelle de Belgique*, 19(35): 1-16.
- Casier, E. 1946. La faune ichthyologique de l'Yprésien de la Belgique. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique*, 104: 1-267.
- Casier, E. 1967. Le Landénien de Dormaal (Brabant) et sa faune ichthyologique. *Mémoire Institut Royal des Sciences naturelles de Belgique*, 156: 3-66.
- Compagno, L. J. V. 1977. Phyletic relationships of living sharks and rays. *American Zoologist*, 17: 303-322.
- Garmen, S. 1913. The Plagiostomia. (Sharks, skates and rays). *Memoirs of the Museum of Comparative Zoology, Harvard College*, 36: 515 pp., 75 pls.
- Herman, J. 1975. Les sélaciens des terrains néocrétacés et paléocènes de Belgique et des contrées limitrophes. Éléments d'une biostratigraphie intercontinentale. *Mémoires pour Servir à l'Explication Cartes Géologiques et Minières de la Belgique, Service Géologique de Belgique*, 15: 1-450.
- Kemp, D., L. Kemp and D. Ward. 1990. *An illustrated guide to the British middle Eocene vertebrates*. Privately published, London, UK, 59 pp.
- Leriche, M. 1902. Les poissons paléocènes de la Belgique. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique*, 22: 1-48.
- Leriche, M. 1905. Les poissons tertiaires de la Belgique. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique*, 3: 49-228.
- Lythgoe, J. and G. Lythgoe. 1992. *Fishes of the sea: the North Atlantic and Mediterranean*. MIT Press, Cambridge, MA, 256 pp.
- Michael, S. W. 1993. *Reef sharks and rays of the world*. Sea Challengers, Monterey, CA, 107 pp.
- Nishida, K. and K. Nakaya. 1990. Taxonomy of the genus *Dasyatis* (Elasmobranchii, Dasyatidae) from the North Pacific. in: H. L. Pratt, Jr., S. H. Gruber and T. Taniuchi (eds.), *Elasmobranchs as living resources: advances in biology, ecology, systematics and the status of the fisheries*. *National Oceanic and Atmospheric Administration Technical Report*, no. 90, pp. 327-346.
- Nolf, D. 1988. *Fossiles de Belgique. Dents de requins et de raies du Tertiaire de la Belgique*. Institut Royal des Sciences naturelles de Belgique, Brussels, Belgium, 184 pp.
- Smith, M. M. and P. C. Heemstra (eds.). 1986. *Smith's sea fishes*. Springer-Verlag, New York, NY, 1047 pp.
- Thurmond, J. T. and D. E. Jones. 1981. *Fossil vertebrates of Alabama*. University of Alabama Press, University, Alabama, 244 pp.
- Timmerman, J. and R. Chandler. 1995. *Cretaceous and Paleogene fossils of North Carolina*. North Carolina Fossil Club, Durham, NC, 70 pp.
- Ursin, M. J. 1977. *A guide to the fishes of the temperate Atlantic coast*. E. P. Dutton, New York, NY, 262 pp.
- Ward, D. J. 1984. Additions to the fish fauna of the English Palaeogene. 5. A new species of *Raja* from the London Clay. *Tertiary Research*, 6: 65-68.

Ward, D. J. and R. L. Wiest, Jr. 1990. A checklist of Palaeocene and Eocene sharks and rays (Chondrichthyes) from the Pamunkey Group, Maryland and Virginia, USA. *Tertiary Research*, 12: 81-88.

Wass, M. L. 1972. *A check list of the biota of lower Chesapeake Bay*. Virginia Institute of Marine Science, Special Scientific Report no. 65, Gloucester Point, VA, 290 pp.

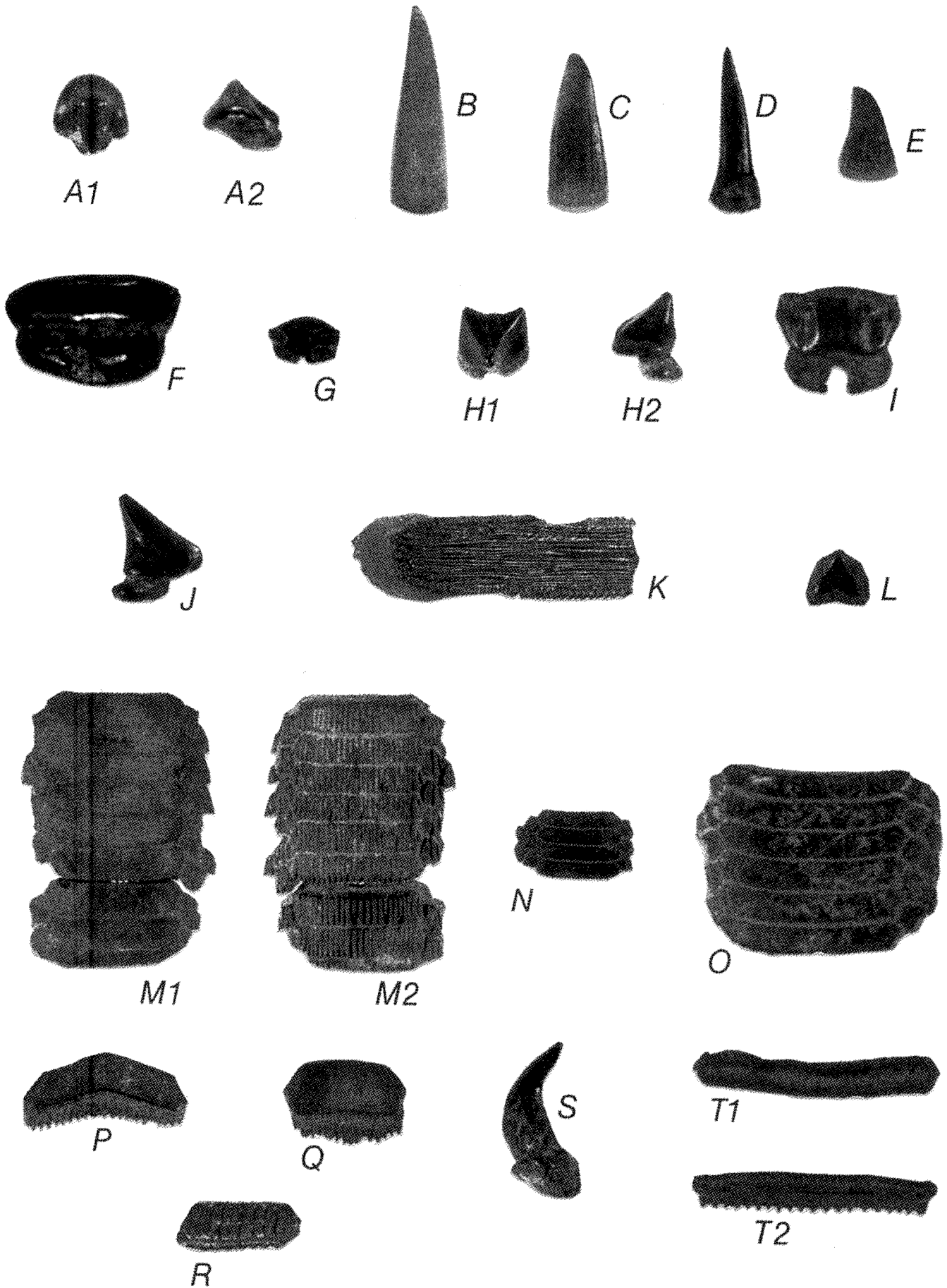
White, E. I. 1926. Eocene fishes of Nigeria. *Bulletin of the Geological Survey of Nigeria*, 10: 1-82.

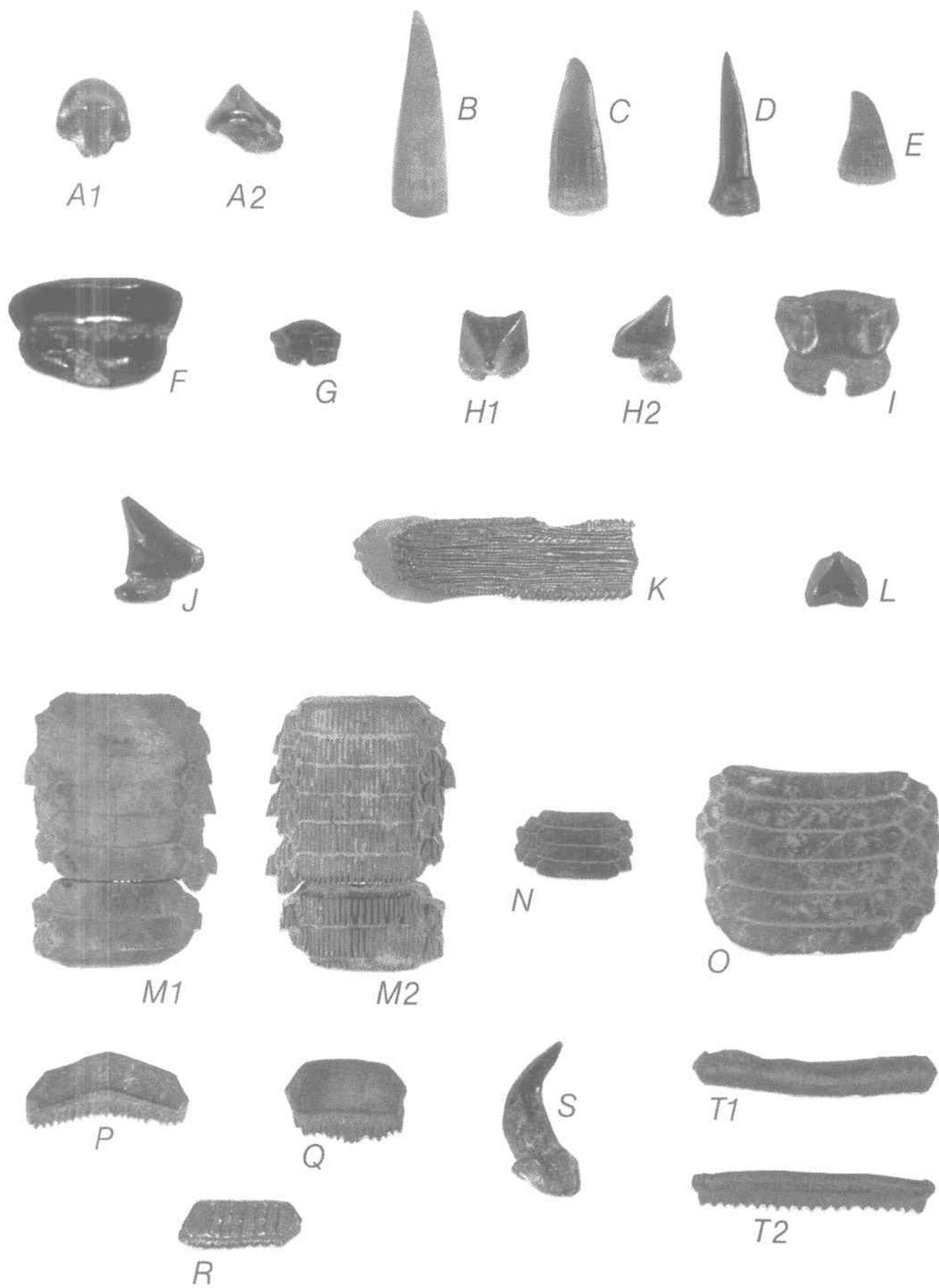
Whitehead, P. J. P., M.-L. Bauchot, J.-C. Hureau, J. Nielsen and E. Tortonese (eds.). 1984. *Fishes of the north-eastern Atlantic and the Mediterranean* (vol. 1). United Nations Educational, Scientific and Cultural Organization (UNESCO), Paris, France, 510 pp.

Woodward, A. S. 1899. Notes on the teeth of sharks and skates from the English Eocene. *Proceedings of the Geological Association*, 16: 1-14.

### Plate 3.1

- A - *Rhinobatos bruxelliensis* tooth; 1 = occlusional view, 2 = profile view; width = 1.8 mm (Gary Grimsley, USNM 496474).
- B - *Pristis lathamii* rostral tooth; dorsal view; height = 39 mm (Mike Folmer, USNM 496475).
- C - *Anoxypristis mucrodens* rostral tooth; dorsal view; height = 30 mm (Mike Folmer, USNM 496476).
- D - *Anoxypristis* sp. rostral tooth; dorsal view; height = 10 mm (Chuck Ball, USNM 496477).
- E - *Propristis schweinfurthi* rostral tooth; dorsal view; height = 18 mm (Mike Folmer, USNM 496478).
- F - *Hypolophodon sylvestris* lateral tooth; lingual view; width = 4 mm (Mike Folmer, USNM 496479).
- G - *Meridania convexa* anterior tooth; lingual view; width = 4.5 mm (Mike McCloskey, USNM 496480).
- H - *Jacquhermania duponti* anterior tooth; 1 = occlusional view, 2 = profile view; height = 2 mm (Mike Folmer, USNM 496481).
- I - *Coupatezia woutersi* lateral tooth; lingual view; width = 3 mm (Chuck Ball, USNM 496482).
- J - *Heterotorpedo fowleri* male anterior tooth; profile view; height = 2.7 mm (Ron Keil, USNM 496483).
- K - Myliobatid caudal spine (basal fragment); dorsal view; length = 55 mm (Mike Folmer, USNM 496484).
- L - Myliobatid dermal thorn; apical view; width = 7 mm (Mark Bennett, USNM 496485).
- M - *Myliobatis dixonii* lower dental plate; 1 = occlusional view, 2 = basal view; length = 50 mm (Mike Folmer, USNM 496486).
- N - *Myliobatis striatus* lower dental plate; occlusional view; length = 13 mm (Mike Folmer, USNM 496487).
- O - *Myliobatis latidens* lower dental plate; occlusional view; length = 17 mm (Mike Folmer, USNM 496488).
- P - *Aetobatis irregularis* lower tooth; occlusional view; width = 16 mm (Mark Bennett, USNM 496489).
- Q - *Aetomylaeus* sp. medial tooth; occlusional view; width = 11 mm (Ron Keil, USNM 496490).
- R - *Rhinoptera sherboni* lateral tooth; basal view; width = 6 mm (Gary Grimsley, USNM 496491).
- S - *Archaeomanta melenhorsti* tooth; profile view; height = 3.5 mm (Mark Bennett, USNM 496492).
- T - *Burnhamia daviesi* medial tooth; 1 = occlusional view, 2 = lingual view; width = 24 mm (Mike Folmer, USNM 496493).







## PART 4. ACTINOPTERYGIAN FISHES FROM THE FISHER/SULLIVAN SITE

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### ABSTRACT

At least 39 kinds of actinopterygian bony fishes are represented at the Fisher/Sullivan site near Fredericksburg, Virginia. Most of these were marine or salt-water tolerant species that normally inhabited the shallow continental shelf environment. Modern relatives of these taxa are overwhelmingly warm temperate to tropical in habitat, indicating that the coastal marine climate in Virginia then was subtropical. The complexion of the fauna is strikingly modern, indicating that the marine bony fishes of the North Atlantic Ocean basin have not been subjected to severe ecologic stress since the early Eocene.

### INTRODUCTION

Actinopterygian bony fishes are the most abundant and diverse group of fish in the world today. Judging from the fossil record, they have maintained this distinction more than 100 million years. Because their bodies contain numerous bones, it would seem logical to expect that they have left an extensive and well documented fossil record. In a few localities around the world, this is true. In the lower to middle Eocene, for example, whole or nearly whole bony fish skeletons are encountered at places such as Monte Bolca in Italy, in the Green River beds in Utah, and occasionally in the London Clay in England. In these cases, fossil remains readily can be compared with modern types of fishes and their taxonomic placement ascertained. As a result, numerous bony fish have been described from these localities, and a great deal has been learned about their former appearance and diversity.

In most sedimentary rocks, however, fossil remains of bony fishes are scattered, and isolated bones are the normal occurrence. In these more typical cases, such as at the Fisher/Sullivan site, it is relatively easy to confirm the presence of bony fishes as a group, but much more difficult to determine precisely which kinds of fish are represented. In these less favorable depositional settings, successful taxonomic identification of bony fish from their skeletal remains depends heavily on finding those particular parts of each kind of fish that are taxonomically distinctive. The majority of isolated actinopterygian bones that are found provide only general taxonomic information.

Often the most distinctive parts of a bony fish are its jaws and teeth. In many cases, however, the jaws are not readily fossilized, the fish had no teeth, or its teeth are very generalized and not distinctive. In such cases, other parts of the skeleton may be more useful, such as the basicranium, dermal armor, fin spines, or specialized structures such as the hypural fans of scombroid fishes. Therefore, it is best to collect any and all remains of bony fish and to sort through

them later for whatever bones are most taxonomically useful. Because bony fishes contain so many bones, and because there literally are thousands of bony fish species living today, the task of sorting and identifying disarticulated material is daunting. Even so, identifications can be made from this kind of material, and the resulting information can expand significantly our understanding of the former diversity and ecology of these creatures.

In all probability, there were many more kinds of actinopterygian fish at the Fisher/Sullivan site than presently can be identified. Based on the known diversity of bony fishes at exceptional Eocene fossil localities, such as at Monte Bolca in Italy where 113 genera of actinopterygian fishes have been identified (Frickhinger, 1995), it seems likely that the 39 kinds of bony fishes recognized at the Fisher/Sullivan site represent only about one-third of the total number of species that were present. Even so, the Fisher/Sullivan site has produced a much richer bony fish fauna than any other locality known from the Pamunkey Group, and the identified species still represent a significant fraction of the total number that probably then existed. These fish remains are described systematically as follows.

**Class Osteichthyes Huxley 1880**  
**Infraclass Actinopterygii Cope, 1887**  
**Order Acipenseriformes Hay, 1930**

Sturgeons are a group of primitive fish found today only in the Northern Hemisphere. All species spawn in fresh water, and many remain in fresh water their entire lives. Individuals of some species, however, migrate to the sea after hatching and spend most of their lives in salt water (Wheeler, 1975).

**Family Acipenseridae Bonaparte, 1831**  
**Genus Acipenser Linnaeus, 1758**  
*Acipenser* sp.

**Figured specimens:** Two fragmentary skull elements (USNM 498659, USNM 498660) collected by Mike Folmer.

**Description:** When seen in cross-section, skull elements composed of stacked thin sheets of bone, internal surface smooth and external surface ornamented with irregular pits and grooves.

**Discussion:** Two skull fragments (Plate 4.10, A-B) are readily assigned to *Acipenser* on the basis of their characteristic surface sculpturing pattern and the sheet-like manner in which the bone was laid down. However, a

species assignment is impossible from such fragmentary material. The figured skull fragments are similar to plates of *Acipenser toliapicus*, described from the London Clay of comparable age, and they may well pertain to that species if it regularly inhabited salt water. The living Atlantic sturgeon (Figure 4.1), for example, probably ranges along both the European and North American Atlantic coasts (Wheeler, 1975). However, until more complete material becomes available, it will remain uncertain if more than one species is represented.



Figure 4.1 The living Atlantic sturgeon *Acipenser sturio* (after Wheeler, 1975).

#### Order Lepisosteiformes Hay, 1926

Gars represent an ancient lineage of highly predaceous actinopterygian fishes that formerly existed in Africa, Asia, and Europe, but today are found only in eastern and central North America and Central America. Despite their dwindling range, gars today are relatively numerous in the eastern and central United States, and alligator gars may reach a length of three meters. They are typically found in fresh water environments, but some species are tolerant of brackish and marine waters (Berra, 1981). The occasional occurrence of isolated gar scales in Paleocene and Eocene shallow marine deposits in the southeastern United States (Case, 1986; Weems, 1998) suggests that some Early Tertiary gars also were salt-water tolerant (euryhaline) or even occasional inhabitants of salt water.

#### Family Lepisosteidae Cuvier, 1825

#### Genus *Lepisosteus* Lacépède, 1803

*Lepisosteus* sp.

**Figured specimens:** One vertebra collected by Tom Parks, one scale (USNM 496296) collected by Mike Folmer, two scales (USNM 496298, USNM 496300) collected by Chuck Ball.

**Supplementary specimens:** Two scales collected by Mike Folmer (USNM 496295, USNM 4962997), one scale (USNM 496299) collected by Chuck Ball.

**Description:** Vertebra anteroposteriorly compressed, with the anterior face convex and the posterior face concave (opisthocoeilus). Scales rhomboidal, thick, and densely bony.

**Discussion:** Tertiary and recent gars were split into two genera (*Atractosteus* and *Lepisosteus*) by Wiley (1976), but Grande (1980) more recently has considered *Atractosteus* to be inadequately defined and has recognized only *Lepisosteus* (Figure 4.2). The latter practice is followed here. An opisthocoeilus

vertebra and isolated thick-boned scales (Plates 4.1, A; 4.2, A-C), recovered from the Fisher/Sullivan site, are characteristic of the Lepisosteidae and *Lepisosteus*, but these remains are inadequate to determine what species is represented.

In western Europe and the southern United States, late Paleocene to middle Eocene scales of this type have been referred to *Lepisosteus fimbriatus* (Wood, 1846) or the junior synonym of that taxon, *Lepisosteus suessionensis* (Leriche, 1900, 1902; White, 1931; Wiley, 1976; Case, 1986; Kemp and others, 1990). However, all available material from those areas is quite fragmentary, and none of it is particularly diagnostic. A number of distinct species of *Lepisosteus* occur in the freshwater lower Eocene Green River Formation of Utah, so it seems reasonable to assume that a comparable diversity of gars may have existed in eastern North America and western Europe. Until better and more complete material is forthcoming, it is impossible to place any particular species assignment on the available fragments.

In the Chesapeake Bay area, fossil remains of *Lepisosteus* so far have been found only in the Potapaco Member of the lower Eocene Nanjemoy Formation and the Piscataway Member of the upper Paleocene Aquia Formation. Remains of *Lepisosteus* also occur widely in Early Tertiary strata of the northern hemisphere and have been reported in the literature from New Mexico (Lucas, 1984), Utah (Wiley, 1976), Montana (Estes, 1976), North and South Dakota (Cvancara and Hoganson, 1993), Texas (Westgate, 1989), Louisiana (Hopkins, 1870), Arkansas (Westgate, 1984), Mississippi (Case, 1986), Alabama (Thurmond and Jones, 1981), South Carolina (Weems, 1998), England (White, 1931; Ward, 1978), France (Casier, 1946), and central India (Gayet and others, 1984). Fossil forms probably were very similar to living forms in appearance (Figure 4.2).



Figure 4.2 The living gar *Lepisosteus osseus* (after Agassiz, 1833-1844).

#### Order Pycnodontiformes Berg, 1940

Pycnodonts first appear in rocks of Jurassic age, and they were common and diverse in marine sediments throughout the remainder of the Mesozoic. Their diversity was greatly reduced at the end of the Mesozoic, with only the genera *Anomoeodus*, *Palaeobalistium*, *Coelodus*, *Nursalia*, and *Pycnodus* surviving into the Tertiary. The last known pycnodonts are from sediments of middle Eocene age (Longbottom, 1984). Two specimens from the Fisher/Sullivan site are the first reported Tertiary occurrence of the group in the Chesapeake Bay region, and both known specimens could have come from a single individual. Even

though pycnodonts were approaching the end of their existence, and they probably were not common in the Pamunkey Group, they have been found widely elsewhere in lower Eocene sediments, including England and Belgium (Casier, 1966), Tunisia and Algeria (Arambourg, 1952), Mali (Longbottom, 1984), Mississippi (Case, 1986), and India (Kumar and Loyal, 1987). Because they have no close living relatives, little is known about their ecology or their habitat preferences.

**Family Pycnodontidae Agassiz, 1832**

**Genus *Pycnodus* Agassiz, 1833**

*Pycnodus* sp.

**Figured specimens:** One tooth (USNM 496218) collected by Jim Savia, anterior vomer(?) collected by Tom Parks.

**Description:** Tooth round to elliptical in oral view and flattened in lateral view; bearing an enamel surface that is smooth, rounded, and unornamented. Pulp cavity shallow and broad.

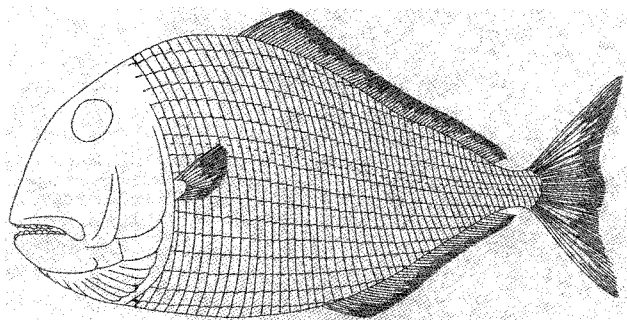


Figure 4.3 Restoration of the body form of *Pycnodus platessus* (after Agassiz, 1833-1844).

**Discussion:** One pycnodont tooth (Plate 4.1, D) and the anterior end of a vomer(?) bearing very worn teeth (Plate 4.7, H) have been identified among the fish remains from the Fisher/Sullivan site. There are three families of pycnodonts currently recognized from the early Eocene (Blot, 1987), but only members of the family Pycnodontidae were large enough to bear teeth such as these. The morphology of these teeth is typical of *Pycnodus*, so they confidently can be referred to that genus. Species level identifications depend heavily on both the relative size and placement of teeth within the splenial and vomerine batteries, however. Therefore, the isolated specimens figured here are inadequate to make a species level identification, at least in the absence of any other well preserved dentitions from the Chesapeake Bay region.

Pycnodont dentitions, although unique in detail, are grossly similar to a number of living fishes that crush hard food such as clams, snails, or coral. Therefore, it is likely that these fish used their teeth for a similar purpose. The manner in which these fish replaced their teeth as they grew is controversial (Longbottom, 1984). However, in at least some species, the teeth in the anterior

portion of the mouth became deeply worn with age, as in the specimen shown in Plate 4.7, H. Complete specimens of *Pycnodus platessus* have been recovered from the Eocene Monte Bolca area in Italy (Agassiz, 1833-44; Blot, 1987) and one of these is shown in Figure 4.3 to give some idea of the body shape of these peculiar and specialized fishes. It is entirely possible that the Fisher/Sullivan specimens pertain to this species, which had teeth very similar in size and shape to the one shown in Plate 4.1.

**Order Amiiformes Huxley, 1861**

The bowfin represents another primitive family of highly predaceous actinopterygian fishes that, like gars, has survived to the present only in eastern and central North America (Berra, 1981). Amioid fishes appear in the Cretaceous, and several fossil Tertiary species have been described. Although most Tertiary fossil species are from North America, fossil bowfins also occur in Europe and Asia. Only one species remains, *Amia calva* (Figure 4.4), which appears to be restricted to fresh water habitats. (Boreske, 1974).

**Family Amiidae Bonaparte, 1837**

**Genus *Amia* Linnaeus, 1766**

*Amia* sp.

**Figured specimens:** Premaxillary bearing teeth (USNM 496216) collected by Mike Folmer, isolated vertebral centrum (USNM 496217) collected by Gary Grimsley.

**Description:** Premaxillary short, suturally attached to antorbital and rostral bones, bearing long, recurved, conical, and pointed teeth. Vertebra strongly compressed anteroposteriorly, laterally elongate, and concave both anteriorly and posteriorly.

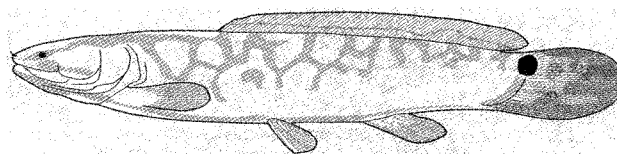


Figure 4.4 The living bowfin, *Amia calva* (after Wheeler, 1975).

**Discussion:** The occurrence of needle-like teeth in a short premaxillary that is suturally attached to surrounding bones (Plate 4.1, B), and the anteroposterior compression and lateral elongation of the vertebra (Plate 4.1, C) are both typical traits of bowfin fishes. However, neither vertebrae nor premaxillaries are among the elements that are useful for determining species level identification (Boreske, 1974). Because all valid Tertiary species are currently assigned to *Amia*, and because the Fisher/Sullivan specimens show no obvious differences from the living genus, these specimens can be assigned to that genus with confidence.

Bowfins today are exclusively freshwater fishes, and they may well have had a similar environmental restriction in the Early Tertiary. However, the persistent though rare occurrence of bowfin remains in Early Tertiary shallow

marine environments suggests that these fishes in the Early Tertiary may have been, like gars, more tolerant of salt-water than the living species and thus capable of wandering into marine environments for prolonged periods of time. Such a tolerance to salt-water would have aided their migration across the North Atlantic corridor in late Paleocene and early Eocene time, and this would help to explain Boreske's (1974) conclusion that *Amia uintaensis* occurs in both France and North America.

**Order Osteoglossiformes Andrews, Gardiner, Miles and Patterson, 1967**

This group of fishes, known as bonytongues, today is restricted to fresh water environments in South America, Africa, Southeast Asia, and northern Australia. Most osteoglossids feed on fish and crustaceans, though the genus *Heterotis* can extract plankton with a helical organ above the gill arches. They have a highly vascularized swim bladder that can function as a lung. These fish generally are large, with adult sizes ranging from one to over three meters (Berra, 1981). Although living forms only inhabit freshwater environments, the fossil genus *Brychaetus* has been found only in marine deposits. Almost certainly it was habitually a marine fish (Taverne, 1978).

**Family Osteoglossidae Bonaparte, 1846**  
**Genus Brychaetus Woodward, 1901**  
*Brychaetus muelleri* Woodward, 1901

**Figured specimens:** Three isolated teeth (USNM 496231, USNM 496250, USNM 496251) and a jaw fragment with four whole teeth and one partial tooth (USNM 498658) collected by Mike Folmer, jaw fragment with six teeth (USNM 496245) collected by Dick Grier.

**Supplementary specimen:** Tooth in jaw fragment (USNM 496279) collected by Mike Folmer.

**Description:** External teeth large, with a lingually recurved shaft and a rectangular basal outline; the enamel cap restricted to the tip of the tooth. Pharyngeal teeth generally smaller and with a rounded root base. Tooth roots hollow.

**Discussion:** Although the family Osteoglossidae today is restricted to freshwater habitats in tropical South America, Africa, South Asia, and Australia, in the Eocene and Paleocene one member of this family, *Brychaetus*, became adapted to marine conditions and spread widely around the Atlantic basin (Casier, 1966; Taverne, 1978). All known occurrences of this fish are from marine deposits. Only the head and the caudal fin region of *Brychaetus* have been described; the central region of the body has not been found intact. For this reason, the fish cannot be accurately reconstructed. However, the living osteoglossid *Heterotis niloticus* (Taverne, 1977) has a very similar head and a

similarly shaped caudal fin (Figure 4.5), so this fish probably provides a good impression of how *Brychaetus muelleri* looked.

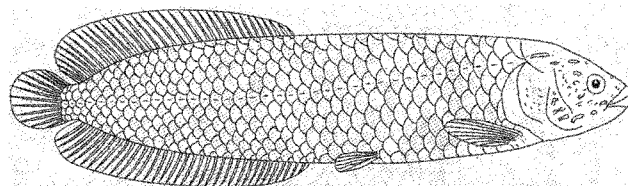


Figure 4.5 The living bonytongue fish, *Heterotis niloticus* (after Taverne, 1977).

Although a dentary of *Brychaetus muelleri* was reported from the overlying Woodstock Member of the Nanjemoy Formation in Maryland (Weems and Horman, 1983), the teeth assigned to this species from the Fisher/Sullivan site represent a downward extension of the range of this taxon and the first occurrence from Virginia. The lingually recurved shaft of the tooth (Plate 4.2, D; 4.10, E), its strongly flattened basal outline, and the enamel cap restricted to the tip of the tooth are distinctive and unlike the teeth of any other early Tertiary fish. It is likely that the tooth illustrated by Arambourg (1952) as *Sparus* instead pertains to *Brychaetus*. Elsewhere, *Brychaetus* is known from the early Eocene of England, Denmark, and Morocco, and from the Paleocene of Cabinda and Nigeria. *Phareodus* is the only other genus in this family that occurs in the Eocene of North America. It is represented by two species that are found in the freshwater Eocene Green River beds of Wyoming (Taverne, 1978).

**Order Elopiformes Greenwood et al., 1966**

The Elopiformes represent a group of primitive teleost fishes that, along with the Anguilliformes and the Notacanthiformes, pass through a distinctive and unique leptocephalus larval stage in their life history. Additionally, they develop rostral ossicles and have the outermost pectoral fin-ray modified into a pectoral splint (Forey, 1973). The order is first known from the Late Jurassic, and appears to have reached its greatest abundance and diversity in the Cretaceous. Four families survived the Mesozoic, and all persist with modest diversity to the present day. These fishes are primarily tropical and marine in distribution (Wheeler, 1975).

**Family Megalopidae Jordan, 1923**  
 gen. et sp. indet.

**Figured specimens:** Two fragments of bony fin rays (USNM 496232, USNM 496233) collected by Mike Folmer.

**Description:** Ray spines consist of three columns of bony segments. The segments comprising the external columns are rectangular, while the medial column consists of segments that are rhomboidal and strongly tilted at an angle. The resulting rows are distinctively torqued and offset.

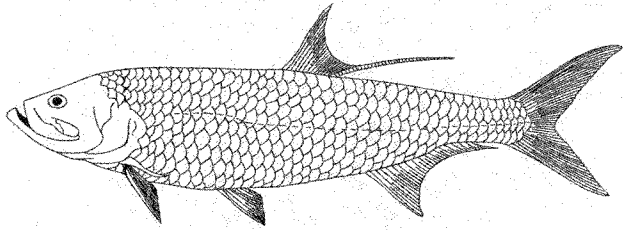


Figure 4.6 The living tarpon, *Tarpon atlanticus* (after Wheeler, 1975).

**Discussion:** Two fragments of bony fin rays (Plate 4.2, E-F) are composed of multiple segments that are strongly torqued. This pattern is rare among living fish, occurring only in megalopids such as *Tarpon atlanticus* (Figure 4.6). Torquing of bone segments within single rays also occurs in *Elops*, which is a member of the closely related family Elopidae, but the intensity of torquing is much less extreme in the Elopidae than in the Megalopidae. Of the two living megalopid genera, *Tarpon* is unknown from the fossil record and *Megalops* is known only as far back as the Pliocene (Robert Purdy, written communication, 1997). However, two fossil genera from this family, *Promegalops* and *Protarpon* (Casier, 1966; Forey, 1973), are known from the lower Eocene London Clay. Probably the fin ray fragments figured here belong to one of these two genera, but both are known only from skull material. Therefore, it is impossible to know which of these genera is represented by these bony ray spines, or even to know if these genera could be distinguished on the basis of fin ray fragments alone. In either case, the fin ray pattern is diagnostic at the family level of taxonomy. The living megalopids are largely tropical in distribution (Wheeler, 1975), suggesting that their Eocene relatives also preferred tropical waters.

#### Family Albulidae Bleeker, 1859

##### Genus *Albula* Scopoli, 1777

*Albula oweni* (Owen, 1840)

**Figured specimens:** Two detached teeth (USNM 496226, USNM 496227) collected by Gary Grimsley, one tooth (USNM 496225) collected by Chuck Ball.

**Supplementary specimens:** Three detached teeth (USNM 496273, USNM 496274, USNM 496275) collected by Mike Folmer; three detached teeth (USNM 496276, USNM 496277, USNM 496278) collected by Chuck Ball.

**Description:** Small, flat-topped, rounded teeth, roughly circular or irregularly polygonal in oral view and about as high as wide in lateral view. Enamel smooth and often heavily worn at the apex of the crown. Root slightly constricted and containing a small shallow pulp cavity.

**Discussion:** A number of flat-topped, rounded crushing teeth were recovered from the Fisher/Sullivan site that can be readily assigned to the genus *Albula*. In life, these teeth are attached to the parasphenoid, endopterygoid, and

basibranchial skull elements (Forey, 1973). After death, they easily become detached and isolated. Most teeth from the Eocene have been assigned to the species *Albula oweni*, which first was described from the lower Eocene London Clay (Casier, 1966). The teeth figured here (Plate 4.1, K-M) are indistinguishable from those assigned to *A. oweni*.

The living *Albula vulpes* (Figure 4.7) is a tropical fish that forages the sea bottom for clams, crabs, shrimp, and occasionally fish (Wheeler, 1975). The striking similarity between the Eocene species and the modern one suggests that both probably had similar habits. This species has been recognized from the lower Eocene of Belgium, England, France, Tunisia, Morocco, Mississippi, and South Carolina (Arambourg, 1952; Casier, 1966; Forey, 1973; Case, 1986; Weems, 1998), and an undescribed species of *Albula* has been figured from the Eocene of Nigeria (White, 1935; Dartevelle and Casier, 1943-1949). In view of its widespread distribution in the Early Tertiary, it is not surprising to find this species in the Chesapeake Bay area.

*Albula eppsi* White and Frost, 1931

**Figured specimens:** Two tooth-bearing skull elements (USNM 496230, USNM 498661), one nearly whole and one fragmentary, collected by Ron Keil and Mark Bennett respectively.

**Description:** Small pharyngeal plates with numerous small tooth sockets of nearly uniform size, a few of which contain very small, flat-topped, rounded teeth, roughly circular or irregularly polygonal in oral view and about as high as wide in lateral view. Enamel smooth and often heavily worn at the apex of the crown.

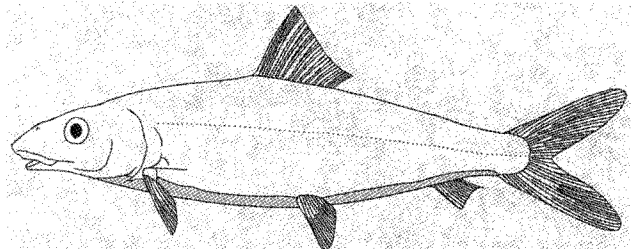


Figure 4.7 The living bonefish, *Albula vulpes* (after Wheeler, 1975).

**Discussion:** Two tooth-bearing skull elements (Plate 4.1, P; Plate 4.12, F) containing small, flat-topped, rounded crushing teeth were recovered from the Fisher/Sullivan site. These can be readily assigned to the genus *Albula*, but not the species *A. oweni*. The fact that the tooth bearing elements are well ossified, yet contain teeth that are much smaller than adult teeth of *A. oweni*, strongly suggests that these elements come from adult fish that were much smaller than adult *A. oweni*. The elements and teeth figured here seem fully comparable to the ones figured by White (1931) and described as *Albula eppsi*, so they are assigned to that species. Casier (1966) synonymized *A. eppsi* with *A. oweni*, apparently on the

assumption that teeth assigned to *A. eppsi* were merely from juvenile *A. oweni*. However, Forey (1973) concluded that the two species were distinct because intermediate sizes of teeth bridging the two size classes were unknown.

*Albula eppsi* has been reported previously from the lower Eocene of England. It was listed by Case (1994) as occurring in Mississippi, but the material he described does not represent an *Albula*. Case's specimens instead should be assigned to *Fisherichthys folmeri*, described below.

#### Family Phyllodontidae Dartevelle and Casier, 1943

Estes (1969) associated the family Phyllodontidae with the Albuloidei on the basis of a similarity in the basibranchial tooth plates and the occlusion pattern of the parasphenoid. Yet Forey (1973) has noted that phyllodontids occur as far back in the fossil record as the Early Cretaceous, which is older than the occurrence of any known albuloid. Additionally, in their tooth replacement pattern, the earlier-appearing phyllodontids are more complex than the later-appearing albuloids. Both of these observations strongly suggest that phyllodontids were not direct descendants of albuloids. It remains plausible that phyllodontids could be elopiform fishes and a sister group to the albuloids. However, because the distinctive phyllodontid tooth plates have never been found associated with any other skeletal elements, such an association cannot be rigorously defended. It remains entirely possible that phyllodontids were holostean or halecostome fishes (Forey, 1973). Whatever their taxonomic affinities, they probably did not survive the Eocene (Estes, 1969).

Because nothing is known of the anatomy of these fish beyond their tooth plates, little can be said about their appearance. Their massive tooth plates clearly indicate that they ate tough food, probably mollusks or other hard-shelled invertebrates. Their relative abundance at the Fisher/Sullivan site, in contrast with the rarity of pycnodontids with similarly massive tooth plates, may indicate that phyllodontids competed successfully with pycnodontids for the same food sources. It is perhaps significant in this regard that phyllodontids and pycnodontids both disappeared toward the end of the middle Eocene.

#### Genus *Egertonia* Cocchi, 1864

*Egertonia isodonta* Cocchi, 1864

**Figured specimen:** Pharyngeal plate with teeth (USNM 496228) collected by Steve Cunningham.

**Description:** Pharyngeal plate bearing numerous, densely clustered, small, rounded, hemispherical teeth. Teeth have a shallow but broad pulp cavity, and replacement teeth are stacked in vertical columns.

**Discussion:** Isolated teeth of *Egertonia* can be confused readily with the marginal teeth of *Phyllodus*, but whole pharyngeal plates lack the large central teeth that characterize

the latter genus. The excellent specimen figured here (Plate 4.1, N) is a typical example of *Egertonia isodonta*, which is the only species recognized in this genus. The presence of shallow, open pulp cavities beneath the teeth and the stacking of replacement teeth in vertical columns serve to distinguish this form from *Paralbula*.

*Egertonia* has been reported from the Paleocene and/or Eocene of England and Belgium, North Dakota, Mississippi, and South Carolina (Casier, 1966; Case, 1986; Cvancara and Hoganson, 1993; Weems, 1998). The Fisher/Sullivan site occurrence extends its range in the Atlantic Coastal Plain northward to Virginia. A probable occurrence of this genus from the middle Eocene of Barbados has been reported by Casier (1959). If that occurrence is valid, it is the latest known occurrence of *Egertonia*.

#### Genus *Phyllodus* Agassiz 1839

*Phyllodus toliapicus* Agassiz, 1839

**Figured specimens:** Three pharyngeal plates with teeth (USNM 496235, USNM 496301, USNM 496302) collected by Mike Folmer, one pharyngeal plate with teeth (USNM 496304) collected by Steve Cunningham, one pharyngeal plate with teeth (USNM 496303) collected by Chuck Ball.

**Description:** Massive pharyngeal plate with sigmoidal curvature, bearing small to large, smooth, flattened teeth that typically are firmly fused to each other and form a mosaic crushing surface. Large teeth are concentrated toward the middle of the plate. Individual teeth have a wide, shallow pulp cavity, and replacement teeth are stacked in vertical columns.

**Discussion:** The unobstructed, broad, and shallow pulp cavity at the base of the teeth and the presence of large, flattened, irregularly shaped medial teeth serve to distinguish this taxon from *Egertonia* and *Paralbula*. In the past, a number of species of *Phyllodus* were erected, but White (1931) demonstrated that these are merely variants among a broad range of possible intergradational morphologies. As a result, all are presently synonymized with *P. toliapicus* (Estes, 1969). Five variants present at the Fisher/Sullivan site are shown (Plate 4.2, H-L) to give a sense of the extreme variability that occurs in this species.

This is the first known occurrence of *Phyllodus* from the lower Eocene Nanjemoy Formation, though it has been reported previously from the underlying upper Paleocene Aquia Formation (Gildersleeve, 1933). Although *Phyllodus* has not been reported from the lower Paleocene Brightseat Formation, its occurrence in the lower Paleocene Tullock Formation of Montana (Estes, 1969) suggests that eventually it may be found there as well. Elsewhere, *Phyllodus toliapicus* has been reported from England, Belgium, France, New Jersey, South Carolina, and Mississippi (Casier, 1966; Estes, 1969; Case, 1986; Weems, 1998).

**Genus *Paralbula* Blake, 1940***Paralbula marylandica* Blake, 1940

**Figured specimen:** Isolated tooth (USNM 496229) collected by Gary Grimsley.

**Supplementary specimen:** Fragmentary pharyngeal plate (USNM 496272) collected by Mike Folmer.

**Description:** Pharyngeal plate bearing numerous small, rounded, smooth, hemispherical teeth. Teeth have a shallow and broad pulp cavity, partially enclosed by a rim of enamel that restricts the opening to the pulp cavity and gives the tooth an appearance similar to a toadstool head. Replacement teeth are stacked irregularly.

**Discussion:** Isolated teeth of *Paralbula* superficially look like teeth of *Egertonia* and the marginal teeth of *Phyllodus*, but the infolding of the enamel about the pulp cavity is characteristic of this taxon and quite unlike the open pulp cavity found in the teeth of the other two genera. Additionally, the irregular stacking of the teeth in the pharyngeal plates stands in marked contrast to the vertically stacked teeth of *Phyllodus* and *Egertonia*. A typical specimen is shown in Plate 4.1, O. Within the genus *Paralbula*, the faintly wrinkled enamel on this specimen distinguishes it from *P. casei* and *P. salvani*.

*Paralbula marylandica* was described originally from the underlying upper Paleocene Piscataway Member of the Aquia Formation of Maryland, so it is not extremely surprising to find that this taxon ranges upward into the overlying lower Eocene Potapaco Member of the Nanjemoy Formation. So far, *Paralbula* is not known from any higher or lower horizon within the Pamunkey Group. The small size of individual teeth, however, make it very possible that it is present at other stratigraphic horizons and simply has not yet been recognized. Teeth similar to *P. marylandica* also have been reported from the middle Eocene of Texas (Westgate, 1989).

**Order Anguilliformes Goodrich, 1909**

The Anguilliformes includes the true eels, which are a distinctive and readily defined group. They pass through a distinctive leptocephalus larval stage that associates them only with the Elopiformes and the Notacanthiformes. From those groups, they are distinguished by a number of anatomical peculiarities, such as the loss of the premaxillaries from the skull and the absence of pelvic fins. Numerous families of living eels have been recognized, but the interrelationships among them remain unclear. The fossil history extends well back into the Cretaceous, and by the early Eocene they already were a diverse and abundant group (Blot, 1978).

**Family Congridae Berg, 1940****Genus *Voltaconger* Blot 1978***Voltaconger latispinus* (Agassiz, 1835)

**Figured specimens:** Partial dentary (USNM 496237) collected by Mike Folmer, partial dentary collected by Tom Parks, partial maxillary (USNM 496224) collected by Gary Grimsley.

**Description:** Dentary and maxillary both bear a single row of teeth, which are stout, closely spaced, and conical to wedge-shaped.

**Discussion:** Three jaw fragments (Plates 4.1, J; 4.2, P-Q) represent a large species of eel. Most eels have multiple rows of teeth, giving their jaw margins a brush-like pattern of teeth rather than the comb-like pattern typical of land animals and scombroid fishes. A few eel genera, however, possess jaws that bear only single rows of teeth, and the specimens described here pertain to one of these. Members of the family Anguillidae all have single tooth rows, as does the genus *Voltaconger* among the Congridae. The tooth morphology of the jaw fragments described here ranges from conical in the front of the mouth to wedge-shaped and closely spaced toward the rear. This pattern is typical of *Voltaconger* and is unlike that documented among the Anguillidae, which have widely spaced conical teeth throughout the mouth (Blot, 1978). Thus the jaw fragments from the Fisher/Sullivan site can be referred to *Voltaconger*, which was described from the middle Eocene Monte Bolca beds of Italy. Although the material from the Fisher/Sullivan site is sparse, there is nothing that would debar it from being assigned to the described species, *Voltaconger latispinus*. A restoration of *Voltaconger* by Blot (1978) is shown in Figure 4.8. The size of the material from the Fisher/Sullivan site suggests that it probably came from an animal slightly less than a meter long.



Figure 4.8 The Eocene eel, *Voltaconger latispinus* (after Blot, 1978).

**Genus *Bolcyrus* Blot, 1978**cf. *Bolcyrus formosissimus* (Eastman, 1905)

**Figured specimen:** Fragment of a dentary (USNM 496220) collected by Gary Grimsley.

**Description:** Dentary elongate and dorso-ventrally thin, bearing a single row of large nutrient foramina on its external margin. Tooth sockets demonstrate the presence of four rows of teeth, the second row from the external margin bearing much larger teeth than the other three rows.

**Discussion:** A second kind of eel is represented among the Fisher/Sullivan site material. This eel is known only from a single lower jaw fragment that lacks teeth (Plate 4.1, F; 4.9, A).

It possesses tooth sockets, however, that clearly define four parallel rows of teeth. This contrasts markedly with the single row of teeth found in *Voltaconger*. One of the four tooth rows, the second from the exterior jaw margin, has sockets that are two to three times wider than those in the other rows. The jaw ramus is long and narrow, and its external margin has a row of prominently large nutrient foramina. These foramina are very similar to, but not exactly identical with, the arrangement of large foramina illustrated on the dentary of *Bolcyrus formosissimus* from Monte Bolca (Blot, 1978). The jaw at hand is not closely comparable to any other described fossil eel, and the number and size pattern of the tooth rows is identical to *B. formosissimus*, so it is tentatively assigned to that taxon (Figure 4.9). It is possible that this specimen pertains to an undescribed species, but if so it cannot be diagnosed adequately on the basis of the scanty material recovered.

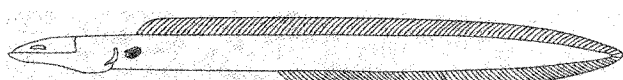


Figure 4.9 The Eocene eel, *Bolcyrus formosissimus* (after Blot, 1978).

#### Order Siluriformes Cuvier, 1817

The Siluriformes includes the numerous and diverse catfishes, which have a number of unique anatomical features including the Weberian ossicle, serrated pectoral fins spines, and barbels on their chins. Most catfish live in fresh water, but members of the family Ariidae normally inhabit saltwater.

#### Family Ariidae Günther, 1864

#### Genus Arius Cuvier and Valenciennes, 1840

?*Arius* sp.

**Figured specimens:** Pectoral fin spine (USNM 496221) collected by Steve Cunningham, pectoral fin spine (USNM 496222) collected by Chuck Ball.

**Description:** Sides of pectoral fin spines irregularly striated. Anterior margin is smooth, while the posterior margin bears a double row of tooth-like serrations.

**Discussion:** Two fragmentary pectoral fin spines (Plate 4.1, G-H) demonstrate the presence of marine catfish at the Fisher/Sullivan site. The absence of tooth-like serrations on the anterior margin of the spines precludes their assignment to the genus *Bagre* and suggests that they might belong to the genus *Arius*. A number of fossil specimens have been ascribed to *Arius* (for example, Leriche, 1900, 1923; Casier, 1946; Westgate, 1989), but none of them bears more than a single row of tooth-like serrations on either the anterior or the posterior edge of the spine. "*Arius*" *egertoni* Dixon, 1850 has a single row of very prominent serrations on both its anterior and posterior border, which would seem to place

it in the genus *Bagre*. The fossil ariid species *Rhineastes peltatus* Cope, 1872 has a dorsal spine with multiple rows of tooth-like serrations on its anterior border (Lundberg, 1975), and the presence of multiple rows of spines suggests that the material figured here could pertain to that genus. However, *Rhineastes* has been reported only from freshwater deposits of the Bridger Formation in Wyoming, and its pectoral fin spine is unknown. Therefore, it seems inadvisable to assign the present specimens to that genus on such tenuous evidence. It seems likely that this material pertains to an undescribed species, but the available remains are too scanty for an adequate diagnosis.

There is a living species of *Arius* that occurs along the North American Atlantic coast, and the fossil form from the Fisher/Sullivan site may have looked similar to it (Figure 4.10). The living species is coastal in its habitat and is common from Virginia southward to Panama. This fish moves in large noisy schools, which primarily frequent sandy-bottomed harbors. There they feed mostly on crabs, shrimp, and occasionally fish (Wheeler, 1975). Fossil specimens of *Arius* have been described from the lower Eocene sediments of France and Belgium (Casier, 1966) and from the middle Eocene of Texas (Westgate, 1989) and England (Kemp and others, 1990).

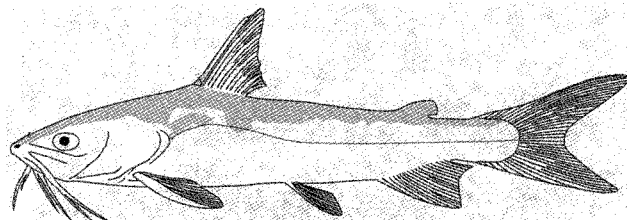


Figure 4.10 The living sea catfish, *Arius felis* (After Wheeler, 1975).

#### Order Aulopiformes Rosen, 1973

The Aulopiformes are an order of fishes that are nearing extinction today, but were abundant and widespread in the Late Cretaceous (Goody, 1969). This group includes the Cretaceous marine family Dercetidae, which presently is composed of three genera of long-bodied and long-snouted fish. *Rhynchodercetis*, the most long-snouted of these taxa, has premaxillaries that are fused into a cylindrical, fluted rostrum (Chalifa, 1989) that is strikingly similar in its form and appearance to the Cretaceous-Tertiary fish rostrum known as *Cylindracanthus*. The dercetids until now have been considered to be a Cretaceous family. It is temporally reasonable to associate the origins of *Cylindracanthus* with the Dercetidae, however, because *Cylindracanthus* is known to range down into the Upper Cretaceous as low as beds equivalent in age (Cenomanian) to those containing *Rhynchodercetis* (Schultz, 1987).

The taxonomic position of *Cylindracanthus* is controversial, in large part because this genus is known only from fragmentary remains. Although other opinions have been

expressed, most authors have assigned *Cylindracanthus* either to the Xiphiidae or to the Blochiidae (see Table 1 in Schultz (1987) for a summary of its taxonomic history). Recently, Schultz (1987) has combined these concepts by placing *Cylindracanthus* in the Blochiidae but at the same time placing the Blochiidae within the Xiphiodea (billfishes). It seems notable to the present author, however, that the rostrum of *Cylindracanthus* bears a striking and detailed resemblance to the rostrum of the Cenomanian dercetid fish *Rhynchodercetis* (Chalifa, 1989), and that the body form of the latter genus also is very similar to that of *Blochius* except for the relative length of the dorsal and anal fins.

These similarities could be explained in one of two ways. Either the similarities between the Dercetidae and the Blochiidae are the result of evolutionary convergence in unrelated groups or the Xiphiodea are derived from the Dercetidae. Of these two choices, convergence between the Dercetidae and the Blochiidae seems more likely because a recent re-evaluation of *Aglyptorhynchus* and *Blochius* by Harry L. Fierstine (personal communication, 1999) has yielded numerous character states in those two genera that relate them closely to the istiophorid and xiphiid billfishes. In turn, blochiids, istiophorids, and xiphiids all have character states that closely ally them with the scombroid fishes. Nothing in their anatomy suggests aulopiform affinities. Therefore, the elongate rostrum of the dercetid *Rhynchodercetis* must certainly be an example of evolutionary convergence between the Dercetidae and billfishes.

Although this much now is clear, the proper taxonomic placement of *Cylindracanthus* remains controversial because only the fused premaxillary bill is known from this fish. Because the morphology of the *Cylindracanthus* bill appears to be more similar to the bill of *Rhynchodercetis* than it is to the bills of *Blochius*, *Aglyptorhynchus*, or *Hemirhabdorrhynchus*, I choose to associate *Cylindracanthus* with the Dercetidae rather than with the Blochiidae. Probably *Congorhynchus* belongs in the Dercetidae as well. Until more complete remains of *Cylindracanthus* and *Congorhynchus* are found, any placement of these genera must necessarily remain tentative. However, the strong similarity between the bills of *Rhynchodercetis* and *Cylindracanthus*, and their common first appearance in the mid-Cretaceous Tethys seaway, do provide plausible evidence for suggesting that they have an intimate relationship.

#### Family Dercetidae Pictet, 1850

#### Genus *Cylindracanthus* Leidy, 1856

*Cylindracanthus rectus* (Agassiz, 1844)

**Figured specimen:** Fragmentary rostrum (USNM 496223) collected by Mike Folmer.

**Description:** Rostrum cylindrical and prominently fluted, with no clear external evidence of bilateral symmetry.

**Discussion:** The fluted, cylindrical shape of the rostrum, combined with the absence of any obvious bilateral symmetry in its external form, are characteristic of this taxon. Only one unequivocal specimen has been found in the Potapaco Member of the Nanjemoy Formation at the Fisher/Sullivan site (Plate 4.1, I). Another specimen, found by Gary Grimsley north of Popes Creek, Maryland, comes from a somewhat higher level of the Potapaco and supports the present identification. This taxon is not known from any older horizons in the Chesapeake Bay area, but previously it has been identified from the overlying Woodstock Member of the Nanjemoy Formation in Maryland (Weems and Horman, 1983).

Only fragmentary remains of this fish have been recovered, but presumably it was similar in appearance to *Rhynchodercetis*, which is known from a complete skeleton found in Israel (Figure 4.11). *Cylindracanthus rectus* also is known from the Carolinas (Fallaw, 1964), Europe (Casier, 1966), and North Africa (Arambourg, 1952). It is reliably known from beds only as young as the upper Eocene. Reports of this genus from the Miocene and Pliocene are highly questionable (Schultz, 1987).



Figure 4.11 The Cretaceous dercetid fish *Rhynchodercetis gracilis* (after Chalifa, 1989).

### Order Perciformes Günther, 1880

The Perciformes include most living bony fishes. The order is characterized, among other things, by the presence of an anterior dorsal fin supported by bony spines, that lies in front of the soft-rayed dorsal fin that also is present in more primitive actinopterygians. Another important feature of this group of fishes is the manner in which the premaxillary has been freed from attachment to the other bones of the skull, rendering it highly mobile (Gregory, 1933). Perciforms apparently evolved in the Mesozoic and underwent an explosive radiation in the Cretaceous. By the beginning of the Cenozoic, they had become the dominant group of marine fishes.

#### Family Serranidae Richardson, 1846

#### Genus *Cyclopoma* Agassiz, 1833

*Cyclopoma folmeri* sp. nov.

**Figured specimens:** Right premaxillary with teeth (USNM 496238) and a vomer (USNM 496236) collected by Mike Folmer.

**Supplementary specimens:** Two right and two left premaxillaries (USNM 498631, USNM 498632, USNM 498633, USNM 498634) collected by Mike Folmer.

**Diagnosis:** So far as known, same as for the genus except that the posterior ascending process of the premaxillary is wide and distally rounded, and the anterior and posterior ascending processes are fused along roughly half their length.

**Description:** Large premaxillary, posterior ascending process wide and distally rounded, anterior ascending process wide and laterally expanded, the two processes closely spaced and fused along roughly half their length. External row of teeth much larger than those in other tooth rows and firmly anchored to jaw. Internal to this tooth row is an area covered with root sockets for a large number of much smaller teeth irregularly arranged in many rows. Vomer broad and anterioroposteriorly shortened, with its anterior margin distinctly triangular in shape.

**Discussion:** The elements assigned to this taxon (Plates 4.2, M; 4.3, A; 4.10, C) are very similar to the comparable elements of living serranids. The size of these specimens indicate that they came from a large fish, and the only described Eocene serranid of comparable size is *Cyclopoma gigas* from Monte Bolca in Italy (Frigo and Sorbini, 1975). In most respects the specimens figured here are similar to *Cyclopoma*, and for that reason they are referred to that genus. However, the posterior ascending process of the premaxillary of *C. gigas* (Figure 4.12) is quite noticeably narrower than that of the specimen figured here, and supplementary specimens consistently show this difference as well. Additionally, the anterior and posterior ascending processes of *C. gigas* appear to be fused only near their base, while the specimens from Fisher/Sullivan site have processes that are fused for about half their length. These differences are sufficient to recognize the Fisher/Sullivan material as a distinct new species, which is named for the discoverer of the type specimen, Mike Folmer.

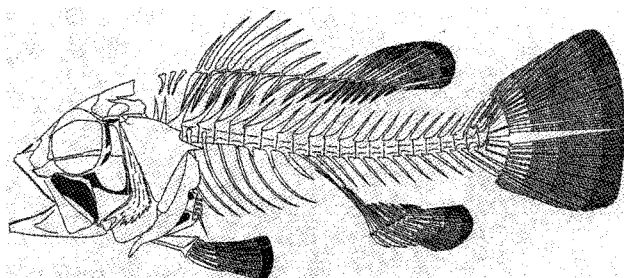


Figure 4.12 The Eocene sea bass, *Cyclopoma gigas* (after Frigo and Sorbini, 1975).

Serranids today are mostly inshore marine fish of bottom-living habits. They are primarily tropical, though some occur in temperate seas. Most are large predatory fish, and some range up to 1,000 pounds in weight (Wheeler, 1975).

**Genus *Prolates* F. Priem, 1899**  
*Prolates dormaalensis* Casier, 1967

**Figured specimens:** Ventral half of a left preopercular

element (USNM 482287) collected by Gary Grimsley.

**Supplementary specimens:** Fragmentary ventral half of a preoperculum (USNM 482288) collected by Gary Grimsley, fragmentary dorsal half of a preoperculum (USNM 482289) collected by Mark Bennett, premaxillary lacking teeth (USNM 482290) collected by Gary Grimsley.

**Description:** Preopercular crescent-shaped and relatively narrow. Ventral border bears four anteriorly directed spike-shaped projections of bone, posterior margin bears numerous short, closely spaced pointed projections arranged in a serrated pattern. Premaxillary similar to that of *Cyclopoma folmeri*, except that it is smaller, has a wider tooth-bearing surface, and does not have an outer row of teeth fused to the premaxillary bone.

**Discussion:** The pattern of four forwardly directed spike-shaped spurs on the ventral border of the preopercular, in conjunction with the serrated posterior margin, is typical of the serranid fish *Prolates dormaalensis* (Casier, 1967), and the specimen figured here (Plate 4.1, E) is close in absolute size to the type of that species. This bone has a shape and pattern that are very different from the preopercular of *Cyclopoma gigas*, so they cannot be ascribed to that genus or species. Additionally, the three partial preopercular specimens and premaxillary here referred to *Prolates* are all from a fish that was much smaller than the serranid remains described above as *Cyclopoma folmeri*. The type specimens of *Prolates dormaalensis* come from the upper Paleocene of Belgium, so the present specimens represent both a range extension across the Atlantic and a temporal extension upward to the lower Eocene for this taxon.

**Family Sparidae Bonaparte, 1831**  
**Genus *Sciaenurus* Agassiz, 1845**  
cf. *Sciaenurus bowerbanki* Agassiz, 1845

**Figured specimen:** Fragmentary dentary lacking teeth (USNM 496246) collected by Mike McCloskey.

**Description:** Dentary deep and short, symphysis long and oriented slightly postero-obliquely; dorsal surface bears a single row of large, round-based, closely spaced teeth.

**Discussion:** The relatively large diameter and rounded shape of the tooth sockets in this jaw fragment (Plate 4.4, D) strongly suggest that it pertains to a sparid fish. As *Sciaenurus bowerbanki* is common and well known from the London Clay (Figure 4.13), the morphology of the dentary of *Sciaenurus bowerbanki* (compare with Casier, 1966) is similar to the morphology of the dentary figured here, and the absolute size of both are comparable, the specimen illustrated here is tentatively referred to that taxon until better material allows a more comprehensive comparison. No teeth have been found as yet that seem

likely to pertain to this fish, though it remains possible that some of the teeth assigned here to *Brychaetus muelleri* might possibly belong to *Sciaenurus* instead.

The Sparidae today includes sea breams, porgies, and snappers. These are marine fish that inhabit tropical to temperate seas. Their diet is varied, including mollusks, sea urchins, crustaceans, squid, and fish (Wheeler, 1975). In view of the absence of molariform teeth in *Sciaenurus*, it seems likely that it fed upon softer prey, such as squid or fish.

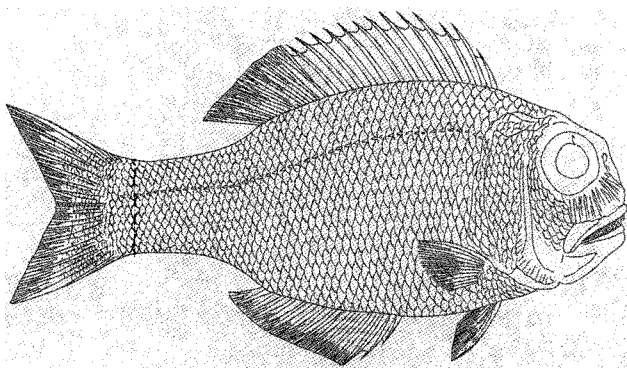


Figure 4.13 The Eocene sparid, *Sciaenurus bowerbanki* (after Agassiz, 1845).

#### Family Sciaenidae? Cuvier, 1829

##### Genus *Fisherichthys* gen. nov.

##### *Fisherichthys folmeri* sp. nov.

**Figured specimen:** Fragmentary pharyngeal plate (USNM 496271), bearing numerous teeth and tooth sockets, collected by Mike Folmer.

**Diagnosis:** The crown of each tooth is triangular in profile view and the underlying root region square to rectangular, giving the entire tooth a pentagonal profile. A grooved rim (cingulum) is present just above the gum line, and a small concave depression is present on the tip of the conical tooth crown. The concave depression is surrounded by a circular array of small, irregular papillae. As the genus is currently monotypic, the diagnosis applies both to the genus and the species.

**Description:** Pharyngeal plate flattened on its oral surface, bearing numerous teeth arranged in an irregular mosaic pattern. Teeth round in oral view, closely spaced or separated by small gaps up to half the diameter of the teeth. Replacement teeth erupt between previously erupted teeth. Tooth sockets round in plan view, with an outer depressed rim of bone, marked by radial striations, for attachment of the overlying tooth. The center of each tooth socket is occupied by a large round foramen, located beneath the presumed position of the pulp cavity of the tooth.

**Discussion:** Although the pharyngeal plate is only fragmentary, the teeth that it bears are very unusual in their morphology (Plates 4.7, D; 4.8, A-B). The broad and

flattened tooth-bearing surface of the pharyngeal plate, as well as the arrangement of the teeth and the pattern of tooth replacement, is reminiscent of the tooth-bearing pharyngeal plates found in the living sciaenid *Pogonias chromis*. For this reason, this specimen is tentatively associated with that family. It is entirely possible, however, that the similarities are the result of convergent evolution rather than any close familial relationship.

With the exception of teeth illustrated by Case (1994), nowhere have I observed fish teeth, fossil or living, that are remotely similar to the teeth of *Fisherichthys folmeri*. Although its teeth have the general appearance of teeth born by fish that crush hard food such as mollusks, sea urchins, or crustaceans, the details of the tooth morphology are very different. It might be argued that the concavity at the conical tip of the tooth is a result of wear due to feeding, but this is contradicted by the fact that unworn teeth just erupting from the pharyngeal plate show this characteristic in a fully developed state. Moreover, the papillae around this concavity shows little sign of wear, even in fully erupted teeth, suggesting that the feeding habits of this fish did not wear the teeth rapidly. The cingulum around the base of each tooth is variable in its degree of development, but typically it is present. None of the teeth can be seen in aboral view, but the presence of a large foramen in the center of the tooth sockets strongly suggests that a pulp cavity is present.

The functional significance of these teeth is puzzling. Their complex but uniform shape clearly had to be determined genetically, and therefore this fish invested a significant fraction of its genome in standardizing the complex developmental pathways needed to produce such a distinctive and uniform pattern. This in turn implies that the shape of these teeth was important for properly processing food. Among human tools, these teeth are most similar to awls, which are designed to punch through a hard surface without smashing it. It is difficult, however, to envision any advantage to such a delicate approach to killing or grasping food. This is even more unlikely in view of the fact that even the most fully erupted teeth show little sign of wear on the papillae surrounding the terminal concavity.

A more likely use for a tooth of this type would be if the prey animal was externally slippery, or else externally soft but internally hard. In such a case, the roughness of the papillae would help to prevent the tooth from slipping off the surface of the prey, while the stout conical shape of the tooth would maximize pressure on the underlying skeleton and help to crush it. The cingulum around the base of the tooth might help to limit how far the tooth would sink into the body of the prey. Such a method of food gathering might be useful in hunting a number of types of marine invertebrates, such as sea cucumbers or smooth-shelled mollusks.

*Fisherichthys* is named in honor of Mr. Dennis Fisher and Mr. Larry Fisher, who kindly allowed the type material to be collected. The species is named for Mike Folmer, who discovered the type specimen. Teeth of comparable age, described from the upper Paleocene and lower Eocene of Mississippi by Case (1994) under

the name *Albula eppsi*, are fully comparable in all observable characteristics to teeth of *Fisherichthys folmeri*. Such teeth are only grossly similar to teeth of *Albula*, and therefore are referred here to *Fisherichthys*.

**Family Sphyraenidae Bonaparte, 1831**

**Genus Sphyraena Schneider, 1801**

*Sphyraena bognorensis* Casier, 1966

**Figured specimens:** Four isolated teeth (USNM 496252, USNM 496253, USNM 496254, USNM 496255) collected by Mike Folmer.

**Description:** Teeth small, pointed, laterally compressed, and blade-like. Anterior margin more strongly recurved than posterior margin.

**Discussion:** Three laterally compressed teeth with a slightly recurved tip (Plate 4.5, C-E) are referred to this taxon because they conform in all observable characters with the type teeth figured by Casier (1966) from the London Clay. These teeth differ from *Sphyraena striata* in their absence of fine striations along their margin, as occurs in modern *Sphyraena*. The absence of striations raises the possibility that they might pertain to a trichiurid, many of which have somewhat similar teeth along the sides and rear of their jaws. However, there is another tooth (Plate 4.5, F), probably from the vomer, which is characteristically sphyraenid and not like the teeth of trichiurids. This tooth differs slightly from the type teeth of *S. bognorensis*, as would be expected from its different position in the mouth, and it is possible that it pertains to a different species than the other three teeth. Nevertheless, that tooth demonstrates that *Sphyraena* is represented among the Fisher/Sullivan site material. In the absence of any compelling reason to dispute Casier's reference of the type teeth of *S. bognorensis* to *Sphyraena*, and because there is no compelling reason to assume that these four teeth represent more than one species, they are here all assigned to the genus *Sphyraena* and referred to the species *Sphyraena bognorensis*.

Living barracudas in the Atlantic basin (Figure 4.14) are voracious predators that eat large quantities of smaller fish. Some are solitary, but others travel in schools. They normally are found in warm temperate to tropical waters. Most seem to prefer inshore shallow waters, but they also can be found on the high seas (Wheeler, 1975).

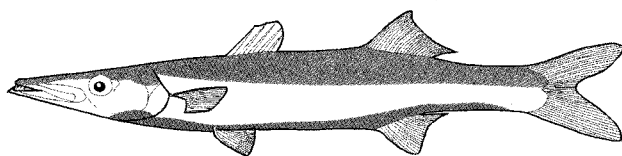


Figure 4.14 The living barracuda, *Sphyraena guachancho* (after Wheeler, 1975).

**Family Gempylidae or Trichiuridae**

**Genus Trichiurides Winkler, 1874**

*Trichiurides sagittidens* Winkler, 1874

**Figured specimens:** Three isolated teeth (USNM 496256, USNM 496257, USNM 496258) collected by Mike Folmer.

**Supplementary specimens:** Seven isolated teeth (USNM 496308-USNM 496314) collected by Mike Folmer.

**Description:** Teeth elongated and recurved posteriorly, shaped in cross-section like a teardrop with the anterior border pointed and blade-like and the posterior border rounded. Base of teeth contain a large and deep, conical pulp cavity. Tip of teeth expanded into a triangle-shaped point.

**Discussion:** A large number of teeth have been recovered from the Fisher/Sullivan site which conform to the above description (Plate 4.5, G-I). As there are numerous teeth of this type, and none of them have the morphologic pattern known as *Eutrichiurides winkleri* or *Trichiurus gulincki*, there are no grounds on which to argue that *Trichiurides sagittidens* is merely a positional variant that belonged in the same mouth as either of the other two taxa. All of the Fisher/Sullivan site teeth are rather small, being less than a centimeter long.

Teeth of this type, originally described from Belgium, have not been found associated with other skeletal materials. Consequently, their taxonomic assignment has been controversial. Winkler (1874) ascribed them to the Trichiuridae, while Leriche (1905) thought that they pertained to the Lophiidae, and Casier (1946, 1966) assigned them to the Merlucciidae. More recently, Cvancara and Hoganson (1993) have placed *Eutrichiurides* in the Trichiuridae. Similar teeth also occur in the family Gempylidae (Nakamura and Parin, 1993). While the possibility of convergent evolution cannot be dismissed out of hand, the teeth are so strikingly trichiurid and gempylid in the details of their appearance that they are here associated with those two closely related families. Unfortunately, distinctions between these two families are based on nondental characters, so in the absence of any other skeletal material it is presently impossible to tell which family is represented.

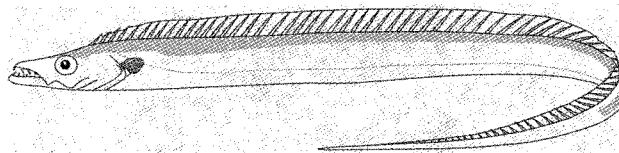


Figure 4.15 The living cutlassfish, *Trichiurus lepturus* (after Wheeler, 1975).

Trichiurids have long, slim, compressed bodies, and their heads and jaws are elongate and armed with large, dagger-like teeth (Figure 4.15). The dorsal fin originates close behind the head and runs the whole length of the back. They inhabit tropical and warm temperate seas and generally are found at

shallow to moderate depths. Although some gempylids are more normally fish-like in their appearance, many are similar in shape to trichiurids. Living gempylids and trichiurids principally eat fish and squid.

**Family Carangidae Gill, 1872**

**Genus *Teratichthys* König, 1825**

*Teratichthys antiquitatus* König, 1825

**Figured specimen:** Left dentary (USNM 498656) collected by Mark Bennett.

**Description:** Dentary deep and strongly recurved toward the midline, interdental symphysis only loosely articulated. Tooth-bearing oral surface flattened and laterally expanded both externally and internally, giving the top of the dentary a "T"-shaped cross-section. Oral surface covered with a myriad of small sockets for numerous rows of teeth.

**Discussion:** The illustration of the type of this species in Casier (1966) does not clearly show the dentary. However, personal observation of the type specimen in the Museum of Natural History in London allows me to state confidently that the dentary of the type specimen compares very favorably to the specimen illustrated here (Plate 4.10, C). The lateral expansion of the flattened tooth-bearing surface, the very numerous tooth sockets and tooth rows, and the deep and recurved jaw ramus are a unique combination of characters that are found in no other fish known from the Early Tertiary of the northern Atlantic Ocean basin.

The living Carangidae include numerous fish that show considerable diversity in their body shapes and lifestyles (Wheeler, 1975). The skull is the only part of *Teratichthys* that has been found, so the rest of the body shape is unknown. For these reasons, it is not yet possible to suggest the body form or ecological preferences for this fish, except to say that it probably was marine.

**Family Pomatomidae Gill, 1865**

**Genus *Sullivanichthys* gen. nov.**

*Sullivanichthys mccloskeyi* sp. nov.

**Figured specimens:** Right dentary (USNM 496244) collected by Mike McCloskey, fragmentary right dentary (USNM 496260) collected by Chuck Ball, right maxillary (USNM 496243) collected by Mike Folmer.

**Diagnosis:** Teeth small, blunt, triangular, and closely spaced. Base of teeth expanded perpendicular to the axis of the tooth row, being about three times wider than long and ovoid in oral view. Top of teeth elongated parallel to the axis of the tooth row, slightly recurved lingually, with a sharp cutting blade developed along the crest of each tooth. Anteriormost tooth somewhat larger and rounder in its basal section than subsequent teeth. More than forty teeth present in each jaw. Anterior teeth are all fully erupted, while only

every second tooth is fully erupted among the posterior teeth. Anterior end of maxillary strongly recurved medially, with the distal end compressed and lacking a nutrient foramen. As the genus is currently monotypic, the diagnosis applies both to the genus and to the species.

**Description:** Dentary short, stout, and deep, bearing a single row of teeth on its dorsal margin. Symphysis vertically oriented and elongate, outer jaw surface sharply angled down and inward, smooth except for several large nutrient foramina mostly concentrated along the lower half of the jaw surface below the jaw angle. The region immediately below the teeth is bowed outward and away from the midline, and a prominent ridge also is developed along the inner margin of the dentary at the same height. Maxillary not attached suturally to surrounding bones, shaft elongate and only slightly expanded posteriorly.

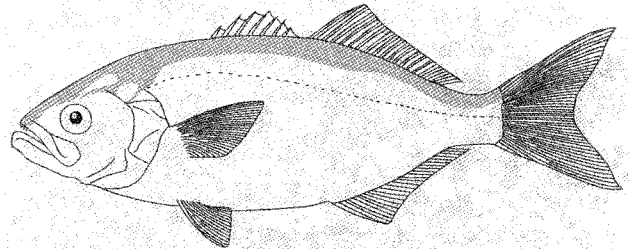


Figure 4.16 The living bluefish, *Pomatomus saltatrix* (after Wheeler, 1975).

**Discussion:** Two dentaries and a maxillary (Plates 4.4, A-B; 4.5, K; 4.8, C-D) are similar except in size to the comparable elements of the living bluefish, *Pomatomus saltatrix* (Figure 4.16). While the general proportions of these bones place them comfortably within this family, the three bones that have been recovered are only about half the size of modern adult *P. saltatrix*, the teeth in the Eocene form are distinctly smaller relative to the size of the jaw than are the teeth in the living genus, and there are about twice as many teeth present in each jaw. Additionally, the living *P. saltatrix* does not have an enlarged tooth at the anterior end of the dentary, and it tends to have only every second tooth fully erupted at any one time. In contrast, the pomatomid remains from the Fisher/Sullivan site possess an enlarged first tooth, have all of the teeth in the front of the jaw fully erupted, and the pattern of every second tooth being fully erupted occurs only in the posterior part of the jaw. Similarly, although the maxillary of the Eocene form is very similar to *Pomatomus* in most respects, it is distinctly more compressed laterally at its distal end than is the maxillary of the living genus, and it lacks the foramen that is typically present in the living form. These differences are sufficiently great to preclude assigning the material at hand to the living genus *Pomatomus*. Consequently, they are assigned to a new genus and species. The nearly complete right dentary is considered to be the holotype, and the fragmentary right dentary and the maxillary are paratypes.

The remains from the Fisher/Sullivan site represent the

oldest occurrence of this family so far reported in the fossil record, and it is quite possible that they represent a form that was ancestral to the living bluefish. The living bluefish occurs widely in tropical and warm-temperate seas. It is a coastal fish, typically found offshore in open water, that travels in large schools, attacking and eating other fish (Wheeler, 1975). The relatively small teeth of the Eocene form suggests that it was not then so strongly adapted to active predation as the modern *Pomatomus*, but otherwise it may have been much like the living member of the family.

*Sullivanichthys* is named in honor of Mr. Russell Sullivan, who kindly allowed the type material to be collected. The species is named for Mike McCloskey, who collected the holotype specimen.

**Family Scombridae Rafinesque, 1815**

**Genus *Acanthocybium* Gill, 1862**

*Acanthocybium proosti* (Storms, 1897)

**Figured specimens:** Left dentary collected by Tom Parks, right dentary fragment (USNM 496266) collected by Ron Harding, dentary(?) fragment (USNM 496267) collected by Ron Harding.

**Supplementary specimen:** Anterior dentary with teeth (USNM 496280) collected by Mike Folmer.

**Description:** Dentary long and slender. Two rows of teeth present, an internal row of very small teeth and an external row of much larger teeth. External teeth closely spaced, stout, triangular, and bearing a thin cutting blade along their external edge. External teeth large in comparison to the size of the dentary.

**Discussion:** Teeth and jaws of this type (Plates 4.3, B; 4.6 E, G) previously have been ascribed to *Cybium* (= *Scomberomorus*). The similarities are real, but in two important characteristics the jaws of the species discussed here are more similar to *Acanthocybium* (see Collette and Russo, 1984, for diagnostic characters of *Scomberomorus* and *Acanthocybium*). First, although the dentary of *Scomberomorus* is thin and long, it is still relatively thicker than the dentary of *Acanthocybium*. In this regard, the jaws of *A. proosti* look much more like *Acanthocybium* than *Scomberomorus*. Second, in living species of *Scomberomorus*, the teeth are replaced in waves so that, at any given time, every other tooth in the tooth row is erupted and the intermediate teeth are unerupted. In contrast, all of the teeth in *Acanthocybium* normally are functional and erupted. The teeth of *Acanthocybium proosti* are, in well preserved jaws, all functional and closely spaced (for example, see Casier, 1966, and Leriche, 1905). It is true that the living species of *Acanthocybium* have teeth that are distinctly stouter than the teeth of *A. proosti*, but it is also true that living species of *Scomberomorus* have teeth that are somewhat less stout. Therefore, *A. proosti* here is

considered to be a somewhat primitive and generalized *Acanthocybium*, rather than a specialized and highly derived *Scomberomorus*.

*A. proosti* constitutes the earliest known occurrence of *Acanthocybium*, and it may well be the ancestor of the living species. It is well known from the Eocene of Europe (Storms, 1897; Leriche, 1905, 1906; Casier, 1946, 1966). The living wahoo, *Acanthocybium solanderi*, is a fast-swimming, open ocean, tropical fish with world-wide distribution (Figure 4.17). Presumably the Eocene species was similar in appearance. It is an active predator that feeds on fish, squid, and cuttlefish (Wheeler, 1975).

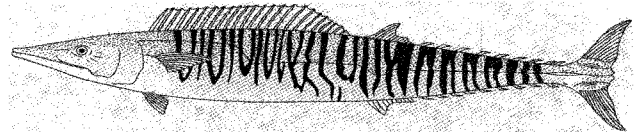


Figure 4.17 The living wahoo, *Acanthocybium solanderi* (after Gregory, 1951).

**Genus *Sarda* Cuvier, 1829**

*Sarda delheidi* (Leriche, 1905)

**Figured specimens:** Anterior end of right dentary collected by Jim Savia, anterior end of left dentary (USNM 496264) collected by Ron Harding, fragment of a premaxillary (USNM 496265) collected by Chuck Ball.

**Description:** Dentary moderately deep and stout. Anterior margin has a long and vertically oriented symphysis. Teeth high, pointed, and rather blade-like. Every other tooth is functional, and the intermediate teeth are unerupted.

**Discussion:** The two fragmentary dentaries are very similar to the type specimen of *Sarda delheidi*, and a premaxillary fragment bears teeth of the same type (Plates 4.5, O-P; 4.6, D). The only possible difference lies in the robustness of the symphysis, but this may well be either an individual or age difference. Another specimen of this species was described from the overlying Woodstock Member of the Nanjemoy Formation of Maryland (Weems and Horman, 1983), so this taxon appears to range throughout the Nanjemoy. In Europe, *Sarda delheidi* is known from Belgium (Leriche, 1905; Casier, 1946). Dental characteristics of the living species of this genus can be found in Collette and Chao (1975).

Living species of *Sarda*, known as bonitos (Figure 4.18), are strong, swift, open-sea predators that travel in compact schools. They normally inhabit warm temperate to tropical

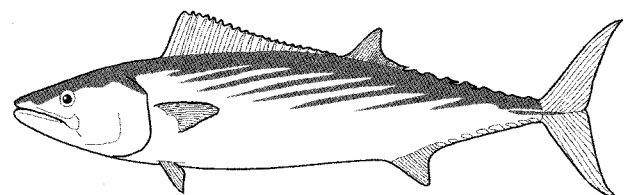


Figure 4.18 The living bonito, *Sarda sarda* (after Wheeler, 1975).

seas, 15 to 20 miles from shore. Their principal prey are fish and squid (Wheeler, 1975).

**Genus *Scomberomorus* Lacépède, 1802**

*Scomberomorus bleekeri* (Storms, 1892)

**Figured specimens:** Three isolated teeth (USNM 496261, USNM 496262, USNM 496263) collected by Gary Grimsley.

**Supplementary specimens:** Eight detached teeth (USNM 496315-USNM 496322) collected by Gary Grimsley.

**Description:** Teeth high and narrow but thick, external edge bears a thin cutting blade. Base of tooth slightly constricted.

**Discussion:** Teeth of this sort (Plate 4.5, L-N) are characteristic of *Scomberomorus bleekeri*. They differ from the teeth of *Acanthocybium proosti* in that they are more elongate, narrower, and have a slight constriction near their base. They differ from *Scomberomorus stormsi* in that they are less elongate, more massive, and have a slight constriction near their base. The original description of this species (Storms, 1892), did not include a good picture of the teeth, but an adequate illustration of a type tooth can be found in Casier (1946).

Living members of *Scomberomorus* go by a number of names, such as mackerel, kingfish, barracuta, katonkel, serra, and cero. The spanish mackerel (Figure 4.19) is typical. These fish are active predators, hunting either singly or in small schools. They primarily feed on smaller fish. Most seem to have seasonal migrations from inshore to offshore and back, and they prefer warm temperate to tropical seas (Wheeler, 1975). *Scomberomorus bleekeri* is known elsewhere from Belgium and France (Storms, 1892; Leriche, 1905, 1906; Casier, 1946).

*Scomberomorus stormsi* (Leriche, 1905)

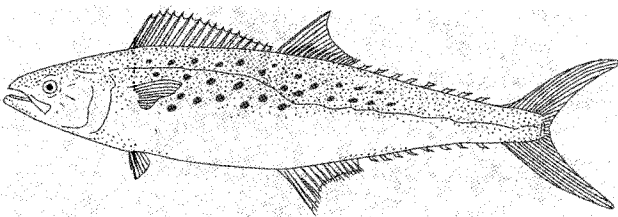


Figure 4.19 The living spanish mackerel, *Scomberomorus maculatus* (after Gregory, 1951).

**Figured specimens:** Left premaxillary and two fragmentary dentaries collected by Tom Parks, well preserved right dentary (USNM 498861) collected by Mike McCloskey.

**Supplementary specimens:** Two dentary fragments (USNM 496287, USNM 496288) and a premaxillary fragment (USNM 496289) collected by Chuck Ball.

**Description:** Premaxillary pointed anteriorly and containing elongate, triangular, thin, blade-like teeth. Dentary contains similar elongate triangular, thin, blade-like teeth. Teeth replaced

in waves, with every other tooth functional at a given time.

**Discussion:** This species is distinguished from *Acanthocybium proosti* and *Scomberomorus bleekeri* by its much thinner and more elongate blade-like teeth. A number of skeletal elements referable to this species have been found at the Fisher/Sullivan site, four of which are illustrated (Plate 4.6, A-C; Plate 4.10, D). It has been previously reported from the early Eocene of Belgium and France (Leriche, 1905, 1906; Casier, 1946). Except for its thinner and more elongate teeth, *Scomberomorus stormsi* probably was very similar in appearance to *S. bleekeri* and living species of this genus (Figure 4.19).

*Scomberomorus* sp.

**Figured specimens:** Right maxillary collected by Tom Parks, hypural fan (USNM 496259) collected by Ron Harding.

**Supplementary specimens:** Hypural fan (USNM 496290) collected by Chuck Ball, hypural fan (USNM 496291) collected by Mike Folmer.

**Description:** Maxillary long and narrow, posterior end broken away. Anterior ascending process elongated and teardrop-shaped, with the narrow end directed anteriorly. Hypural fan posteriorly rounded, ridges run from midline both upward and downward in a postero-oblique direction.

**Discussion:** The shape and proportions of the maxillary (Plate 4.6, F) readily place it in the genus *Scomberomorus*, but it is not clear whether it pertains to *S. bleekeri* or *S. stormsi*. The hypural fan of *Scomberomorus* is rather similar to that of *Acanthocybium*, but direct comparison of the specimen figured here (Plate 4.5, J) with hypural fans of species of both genera indicate that this specimen is closer in its proportions to *Scomberomorus*. In *Scomberomorus*, the posterior margin of the hypural fan is rounded or only slightly elongated, making its posterior margin blunt and its outline rather triangular. In *Acanthocybium*, the posterior margin of the hypural fan is distinctly elongated at the midline, making its posterior margin clearly angled and the entire fan rather diamond-shaped. As with the maxillary specimen, there is no way at present to know if this bone should be referred to *S. bleekeri* or *S. stormsi*.

**Genus *Scombrinus* Woodward, 1901**

*Scombrinus* sp.

**Figured specimens:** A left premaxillary fragment (USNM 498652) and a right(?) dentary fragment (USNM 498653) collected by Mike Folmer.

**Supplementary specimens:** Two right premaxillary fragments (USNM 498654 and USNM 498655) and a dentary fragment (USNM 496290) collected by Mike Folmer.

**Description:** Ramus of premaxillary rounded and elongate,

anterior ascending region low and rectangular-shaped. Dentary and premaxillary both contain a single row of relatively large teeth, many of which are fused into their sockets. Teeth conical and striated around their base. Bone surface striated to rugose.

**Discussion:** The presence of a single row of relatively large and socketed teeth, in addition to the rather low and squared shape of the ascending region of the premaxillary, clearly indicates that these remains pertain to a scombrid fish. Two scombrids from the London Clay have vertically striated teeth, *Scombrinus* and *Scombramphodon*, but the genus *Scombramphodon* possesses two rows of teeth. Therefore, the remains illustrated here (Plate 4.12, D-E) are referred to *Scombrinus*, which has only a single row of teeth. Two species of *Scombrinus* have been recognized from the London Clay, *S. nuchalis* and *S. macropomus* (Casier, 1966). The scanty material so far available is inadequate to determine if these remains pertain to either of these species.

**Family Blochiidae Woodward, 1901**

**Genus Aglyptorhynchus Casier, 1966**

*Aglyptorhynchus veneblesi* Casier, 1966

**Figured specimens:** Fragmentary rostrum (USNM 496234) collected by Mike Folmer, fragmentary rostrum (USNM 496242) collected by Gary Grimsley, vertebra (USNM 496239) collected by Mike Folmer, vertebra (USNM 496240) collected by Gary Grimsley, hypural fan (USNM 496241) collected by Ron Harding, hypural fan collected by Tom Parks.

**Supplementary specimens:** Two hypural fans (USNM 496284, USNM 496285) collected by Mike Folmer, one hypural fan (USNM 496286) collected by Chuck Ball.

**Description:** Body size small. Rostrum distinctly bilateral, dorsally rounded with shallow longitudinal grooves on the dorsal surface. Numerous small teeth present along the ventrolateral margins. Vertebrae elongate and typically xiphioid. Hypural fan triangular, lateral edges nearly smooth.

**Discussion:** Remains of small billfishes are moderately abundant at the Fisher/Sullivan site, only a few of which are illustrated here. The figured rostral fragments (Plates 4.2, G; 4.3 G) are identical in their size and morphology to the rostra of *Aglyptorhynchus veneblesi*, described by Casier (1966) from the London Clay. They differ from *A. sulcatus* in that the dorsal surface of the rostrum of the latter species is marked by a midline depression that makes it appear distinctly bilobed. Two xiphioid vertebrae and two hypural fans (Plate 4.3, C-F) also are figured. They are referred tentatively to this taxon because they pertain to a billfish that was about the same size as *A. veneblesi*. In the absence of any other evidence to suggest that a second small xiphioid species was present, it seems best for now to assume that only one species is represented.

*Aglyptorhynchus* makes its first appearance in the fossil record in the early Eocene and is last seen in the middle Oligocene. Harry L. Fierstine (personal communication, 1999) is in the process of describing a new species of *Aglyptorhynchus* and comparing it to *Blochius*. On the merit of his insightful observations, *Aglyptorhynchus* here is retained in the Blochiidae rather than placed in the Tetrapturidae as advocated by Schultz (1987).

**Incertae sedis**

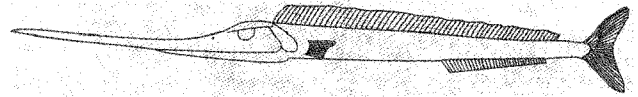


Figure 4.20 The Eocene billfish, *Blochius longirostris* (after Schultz, 1987).

The following nine kinds of fish are tentatively placed within the order Perciformes. They are not scombrids and most may be percoids, but beyond this their taxonomic placement is presently indeterminate. Whatever their exact affinities, they represent species of bony fish that are different from the ones described elsewhere in this article. A summary of the characteristics of the eight taxa described below from premaxillary specimens (Percomorphs B-I) is given in Table 1.

**Percomorph A**

**Figured specimen:** Fused pharyngeals (USNM 496247) collected by Mike Folmer.

**Description:** Very stout, fused pharyngeal plates bearing a flat, circular surface on their oral face that contained a cluster of closely spaced teeth.

**Discussion:** This specimen (Plates 4.4, E; 4.9, C) is very different from anything else that has been recovered from the Fisher/Sullivan site, and nothing like it seems to have been figured in the literature. Unfortunately, the specimen does not retain any teeth, though sockets on the bone indicate that it bore a great many which were closely spaced together. The general morphology of this specimen is reminiscent of similar structures that are found in various genera of the Labridae, Sciaenidae, and other families, but there is no obvious close affinity to any of them. Whether the specimen belongs within one of these living families, or to an extinct family, will remain indeterminate until more complete remains are found.

**Percomorph B**

**Figured specimens:** Two left premaxillaries lacking teeth (USNM 496268, USNM 496269) collected by Mike McCloskey, one right premaxillary lacking teeth and slightly damaged at its anterior end (USNM 498635)

**Table 1. Summary of differences between premaxillaries of Percomorphs B through I**

Percomorph	# of tooth Rows	ramus shape	ramus length	bone sculptured	posterior ascending process	anterior ascending process	other
B	4-8	~straight	long	yes	high & narrow	tilted forward & blade-like	dorsal ramus deeply grooved
C	~3	~straight	long	no	low, wide, rounded	elongate & narrow	anterior process higher
D	~6	curved	short	no	tall, rounded, blade-like	?	external ramus grooved, distinct lip between tooth rows and posterior ascending processes
E	2-3	curved	medium	no	tall, rounded, postero-oblique tilt	tall, slight anterior tilt	anterior & posterior processes fused
F	~8	~straight	short	no	short & rounded	?	external ramus deeply grooved
G	~6	curved	short	yes	thick, narrow, rounded	?	enlarged teeth in external row
H	1	curved	long	no	short, wide, blade-like, rounded	conical, pointed, straight	anterior & posterior processes fused
I	1	straight	medium	no	moderately tall & rounded	tall, nearly vertical	ramus expanded dorso-ventrally in mid-shaft

collected by Mike Folmer.

**Supplementary specimens:** Two left and two right premaxillaries lacking teeth (USNM 498636, USNM 498637, USNM 498638, USNM 498639) collected by Mike Folmer.

**Description:** Premaxillary with its ascending processes moderately wide, distally rounded, and widely divergent; premaxillary ramus deeply grooved on its dorsal surface, only slightly curved, elongated, and distally expanded. Tooth sockets indicate the presence of four to eight poorly defined rows of teeth.

**Discussion:** These elements of a small fish are unlike any other fish remains from the Fisher/Sullivan site (Plates 4.7, A,B; 4.9, B,D; 4.12, A). The specimens have a number of distinctive characteristics. The multiple tooth rows, the deep dorsal groove in the jaw ramus, and the wide divergence of the two ascending processes of the

premaxillary are especially distinctive. This combination of traits could not be found in any of the modern skeletal materials that are available in the U.S. National Museum collections. Not all percoid families are represented, however, so it remains uncertain if these bones pertain to a living family that is unrepresented in the osteological collections, or if they pertain to a family that is now extinct.

#### Percomorph C

**Figured specimen:** Left premaxillary lacking teeth (USNM 496270) collected by Mike Folmer.

**Description:** A left premaxillary with the anterior ascending process of the premaxillary elongate and narrow. The posterior ascending process is moderately wide, rounded, and lower than the anterior ascending process. The two processes are only narrowly divergent. Tooth sockets indicate that there were three rows of teeth present in the jaw.

**Discussion:** This premaxillary (Plate 4.7, C) is quite different from Percomorph B in its morphology, and obviously pertains to a very different and somewhat larger kind of fish. The elongate and narrow anterior ascending process of the premaxillary suggests that this specimen might belong to a primitive scorpaenoid fish, but this is not at all certain.

#### Percomorph D

**Figured specimen:** Right premaxillary lacking teeth (USNM 498640) collected by Mike Folmer.

**Supplementary specimens:** Two left and two right premaxillaries lacking teeth (USNM 498641, USNM 498642, USNM 498643, USNM 498644) collected by Mike Folmer.

**Description:** Posterior ascending process of the premaxillary tall, rounded, and blade-like, anterior ascending process not preserved. Jaw ramus short, tall, and strongly curved, with sockets for about six rows of teeth. The external border of the ramus is deeply grooved and has a distinct lip or bulge immediately above the tooth rows. Bone surface is smooth.

**Discussion:** The great depth and short length of these premaxillaries (Plate 4.11, C) suggest that the fish that possessed them had a powerful bite. This fish is not readily confused with any of the other percomorphs described here, except possibly for Percomorph F which also possesses a deeply grooved external premaxillary ramus. The shape of the posterior ascending process and the presence of a distinct lip immediately above the tooth rows, however, readily distinguish the two forms.

#### Percomorph E

**Figured specimen:** Right premaxillary lacking teeth (USNM 498645) collected by Mike Folmer.

**Description:** Anterior ascending process of the premaxillary tall and slightly tilted anteriorly, posterior ascending process tall, rounded, and tilted slightly posteriorly. Posterior and anterior processes fused along most of their length. Jaw ramus moderately long, moderately high, and slightly curved, with sockets for two to three rows of teeth. Bone surface is smooth.

**Discussion:** This specimen is the only one known representing this taxon (Plate 4.11, D). It is unlike the other taxa listed here except for Percomorph H, which also has fused ascending processes. It differs from that taxon in that it has more than one row of teeth and the shape of the ascending processes are distinctly different.

#### Percomorph F

**Figured specimen:** Right premaxillary lacking anterior ascending process and teeth (USNM 498648) collected by Mike Folmer.

**Supplementary specimens:** Two right premaxillaries lacking anterior ascending process and teeth (USNM 498646, USNM 498647) collected by Mike Folmer.

**Description:** Posterior ascending process of the premaxillary short, rounded, and blade-like, anterior ascending process not preserved. Jaw ramus short, moderately tall, and only slightly curved, with sockets for about eight rows of teeth. The external border of the ramus is deeply grooved. Bone surface is smooth.

**Discussion:** This fish premaxillary (Plate 4.11, E) is not readily confused with any of the other percomorphs described here, except possibly for Percomorph D which also possesses a deeply grooved external premaxillary ramus. The shape of the posterior ascending process and the lack of a lip above the tooth rows in Percomorph F distinguish the two forms.

#### Percomorph G

**Figured specimen:** Left premaxillary fragment lacking posterior end of ramus, anterior ascending process, and teeth (USNM 498649) collected by Mike Folmer.

**Description:** Posterior ascending process of the premaxillary thick, narrow, and rounded, anterior ascending process not preserved. Jaw ramus short, moderately tall, and strongly curved, with sockets for about six rows of teeth. External row of teeth much larger than those in the other five rows. Bone surface is strongly striated.

**Discussion:** This unique fish premaxillary fragment (Plate 4.12, C) is not readily confused with any of the other percomorphs described here, except possibly for *Cyclopoma folmeri*, which also has an enlarged outer row of teeth. It differs from that taxon, however, in its strongly sculptured surface texture and its much shorter and more sharply recurved jaw ramus.

#### Percomorph H

**Figured specimen:** Right premaxillary lacking teeth (USNM 498657) collected by Mike Folmer.

**Description:** Premaxillary with the posterior ascending process of the premaxillary short, wide, rounded, and blade-like, anterior ascending process conical, pointed, straight, and tilted slightly forward. Anterior and posterior ascending processes fused along most of their length. Jaw ramus long, narrow, and strongly curved, with sockets for only one row of teeth. Bone surface smooth.

**Discussion:** This unique fish premaxillary fragment (Plate 4.12, B) is not readily confused with any of the other percomorphs described here, except possibly for Percomorph E which also has its anterior and posterior ascending processes fused along most of their length. It differs from that taxon in the shape of the ascending processes and by the fact that it has only one tooth row.

#### Percomorph I

**Figured specimens:** One right and one left premaxillary lacking teeth (USNM 498650, USNM 498651) collected by Mike Folmer.

**Description:** Premaxillary with the posterior ascending process of the premaxillary moderately tall and rounded, anterior ascending process tall and nearly vertical in orientation. Jaw ramus moderately long, nearly straight, and dorso-ventrally expanded in the mid-shaft region. Tooth sockets present for only one row of teeth. Bone surface smooth.

**Discussion:** These two premaxillaries (Plate 4.11, A-B) are not readily confused with any of the other percomorphs described here, except possibly for Percomorph H, which also has only a single row of teeth. In all other characteristics except bone surface texture, however, they differ.

#### Order Tetraodontiformes Berg, 1940

This order includes such bizarre fish families as the triggerfishes, pufferfishes, boxfishes, and ocean sunfishes. Unlike most fish, members of this group use the caudal fin as a rudder at low speed and rely primarily on their pectoral, dorsal, and anal fins for locomotion. Many members of this group have the mouth modified into a beak.

#### Family Ostraciidae Tyler, 1980 gen. et sp. indet.

**Figured specimens:** Two isolated dermal plates (USNM 496292, USNM 496293) collected by Mike Folmer, one isolated dermal plate (USNM 496294) collected by Chuck Ball, one isolated dermal plate collected by Gary Grimsley.

**Description:** Polygonal dermal plates, smooth on their internal surface and ornamented on their external surface with irregularly scattered rounded papillae. On some plates, the central papilla is largest. Lateral borders often sutured for attachment to adjacent plates.

**Discussion:** A number of isolated dermal plates from the Fisher/Sullivan site (Plate 4.2, N-O; Plate 4.7, E-G) obviously pertain to a species of boxfish. Two families of boxfish are known, the Aracanidae and the Ostraciidae (Tyler, 1980). On the basis of dermal armor plates, the two families can be

distinguished readily by the fact that, on each bony plate, the Aracanidae have a very large central hump or spine from which radiates six "spokes" composed of rows of moderately large papillae. Between these rows of large papillae are fields of much smaller papillae. In contrast, the Ostraciidae lack spines in the centers of their bony plates and the papillate patterns are not organized into discrete spokes as they are on the plates of the aracanids. The plates described here are clearly ostraciid in pattern. Within this family, however, there is considerable diversity of pattern among genera, from area to area of the body of single individuals, and even with age (Winterbottom and Tyler, 1983; Tyler and Gregorova, 1991). Because no well preserved articulated specimens of ostraciids are known from the Paleocene or Eocene of the Atlantic Coastal Plain, there is no way to know even by inference if these isolated plates could be referred to any particular genus or species in that family.

Similar ostraciid plates have been described from the upper Paleocene Aquia Formation of Virginia under the name *Ostracion meretrix* (Leriche, 1942), and from the Paleocene of South Carolina (Weems, 1998). It is quite possible that all of this material represents a single taxon, though there is no way at present to be certain of this. Elsewhere, Early Tertiary ostraciid remains have been described from the lower Paleocene of Morocco (Herman, 1972), the lower Paleocene of India (Gayet and others, 1984), the lower Eocene of England (Tyler and Gregorova, 1991), and the middle Eocene of Italy (Tyler, 1975). The Italian material, known as *Eolactoria sorbinii*, is the only Eocene occurrence that can be adequately diagnosed. It is shown in Figure 4.21.

#### CONCLUSIONS

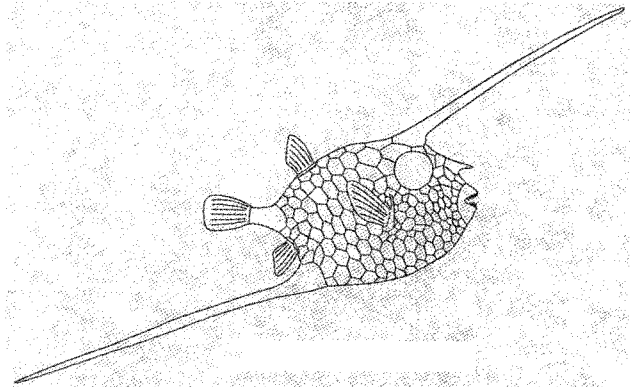


Figure 4.21 The Eocene boxfish, *Eolactoria sorbinii* (after Tyler, 1975).

Bony fishes are represented at the Fisher/Sullivan site by a minimum of 39 species. By comparison with the 113 actinopterygian fish genera known from the well studied middle Eocene Monte Bolca site in Italy, it seems likely that the species found at the Fisher/Sullivan site represent only about one-third of the total number of species that once inhabited the locality. Even so, the known fauna is diverse

enough to draw some general conclusions as to the climatic and ecologic setting then prevailing.

The bony fish fauna clearly is dominated by species that preferred tropical to warm temperate waters (Table 2). Although five taxa could be compatible with a cool temperate climate (*Acipenser*, *Lepisosteus*, *Amia*, and probably *Eutrichiurides winkleri* and cf. *Sciaenurus bowerbanki*), all of these except *Acipenser* also are common in warm temperate and even tropical climates. Thus only *Acipenser*, based on its present range, would not be found in a fully tropical climate. The overwhelming preponderance of both tropical and warm temperate species strongly suggests that the coastal waters of Virginia in the early Eocene were subtropical, perhaps much like the coastal waters of present day central to southern Florida.

**Table 2. Climatic preferences of the bony fishes from the Fisher/Sullivan site**

	Tropical	Warm Temperate	Cool Temperate	Unknown
<i>Acipenser</i> sp.		X	X	
<i>Lepisosteus</i> sp.	X	X	X	
<i>Pycnodus</i> sp.				X
<i>Amia</i> sp.	X	X	X	
<i>Brychaetus muelleri</i>	?	?		
Megalopidae, gen. et sp. indet.	X			
<i>Albula oweni</i>	X	X		
<i>Albula eppi</i>	X	X		
<i>Egertonia isodonta</i>				X
<i>Phyllodus toliapicus</i>				X
<i>Paralbula marylandica</i>				X
<i>Voltaconger latispinus</i>	?	?		
cf. <i>Bolcyrus formosissimus</i>	?	?		
? <i>Arius</i> sp.	X	X		
<i>Cylindracanthus rectus</i>				X
<i>Cyclopoma folmeri</i>	?	?		
<i>Prolates dormaalensis</i>	?	?		
cf. <i>Sciaenurus bowerbanki</i>	?	?	?	
<i>Fisherichthys folmeri</i>				X
<i>Sphyaena bagnorensis</i>	X	X		
<i>Trichiurides sagittidens</i>	?	?	?	
<i>Teratichthys antiquitatus</i>				X
<i>Sullivanichthys mccluskeyi</i>	?	?		
<i>Acanthocybium proosti</i>	X			
<i>Sarda delheidi</i>	X	X		
<i>Scomberomorus bleakeri</i>	X	X		
<i>Scomberomorus stormsi</i>	X	X		
<i>Scombrinus</i> sp.				X
<i>Aglyptorhynchus veneblesi</i>	?	?		
Percomorph A				X
Percomorph B				X
Percomorph C				X
Percomorph D				X
Percomorph E				X
Percomorph F				X
Percomorph G				X
Percomorph H				X
Percomorph I				X
Ostraciidae, gen. et sp. indet.	X	X		
<b>Totals</b>	<b>20</b>	<b>20</b>	<b>5</b>	<b>17</b>

The habitats that are known or inferred for the bony fishes from the Fisher/Sullivan site also indicate that the depositional environment was located in a shallow coastal shelf setting (Table 3). Although two of the taxa might also occur in a deep sea setting, and eight taxa often occur in open ocean settings, all but one (*Acanthocybium*) are typically inhabitants of shallow coastal seas, and ten taxa would not be expected to occur anywhere else. Conversely, except for *Amia*, there are no fish that today are strictly associated with freshwater habitats. Therefore, although the depositional setting was in shallow marine waters, it does not seem to have been so far inshore as to represent an embayment or estuary.

The closest similarities of the Fisher/Sullivan site fauna are with the fish faunas of Europe, especially those from the London Clay in England and from Monte Bolca in Italy (Table 4). Nearly seventy percent of the Fisher/Sullivan site fauna is known to occur on both the eastern and western sides of the North Atlantic. In contrast, only a few species

**Table 3. Habitat preferences of the bony fishes from the Fisher/Sullivan site**

	Coastal	Open Sea	Deep Water	Unknown
<i>Acipenser</i> sp.	X			
<i>Lepisosteus</i> sp.	X			
<i>Pycnodus</i> sp.	?			
<i>Amia</i> sp.	?			
<i>Brychaetus muelleri</i>	?			
Megalopidae, gen. et sp. indet.	X	X		
<i>Albula oweni</i>	X			
<i>Albula eppi</i>	X			
<i>Egertonia isodonta</i>				X
<i>Phyllodus toliapicus</i>				X
<i>Paralbula marylandica</i>				X
<i>Voltaconger latispinus</i>	?			
cf. <i>Bolcyrus formosissimus</i>	?			
? <i>Arius</i> sp.	X			
<i>Cylindracanthus rectus</i>				X
<i>Cyclopoma folmeri</i>	?			
<i>Prolates dormaalensis</i>	?			
cf. <i>Sciaenurus bowerbanki</i>	?		?	
<i>Fisherichthys folmeri</i>				X
<i>Sphyaena bagnorensis</i>	X	X		
<i>Trichiurides sagittidens</i>	?	?	?	
<i>Teratichthys antiquitatus</i>				X
<i>Sullivanichthys mccluskeyi</i>	?	?		
<i>Acanthocybium proosti</i>		X		
<i>Sarda delheidi</i>	X	X		
<i>Scomberomorus bleakeri</i>	X	X		
<i>Scomberomorus stormsi</i>	X	X		
<i>Scombrinus</i> sp.				X
<i>Aglyptorhynchus veneblesi</i>	?			
Percomorph A				X
Percomorph B				X
Percomorph C				X
Percomorph D				X
Percomorph E				X
Percomorph F				X
Percomorph G				X
Percomorph H				X
Percomorph I				X
Ostraciidae, gen. et sp. indet.	X			
<b>Totals</b>	<b>22</b>	<b>8</b>	<b>2</b>	<b>16</b>

occur both in Virginia and in the American Gulf Coast, Africa, and India. It is not at all clear, however, if these lesser similarities reflect a real difference in faunal provinces, or whether they simply reflect the lesser degree to which Gulf Coast, African, and Indian Eocene fish faunas have been sampled.

Of the 39 species of bony fish represented at the Fisher/Sullivan site, 24 belong to living families and 11 of these also belong to living genera (Table 5). Only six species can be assigned definitely to extinct families. Four of these taxa, belonging to the extinct families Pycnodontidae and Phyllodontidae, have teeth that suggest they were bottom-dwelling crushers of hard-shelled invertebrates. Both families died out toward the end of the middle Eocene, and it is possible that their extinction involved some kind of mid-Eocene crisis in the ocean bottom habitat. It seems more likely, however, that these two families simply were displaced by more efficient competitors among the Sciaenidae, Labridae, and Diodontidae. Similarly, the disappearance of the families Dercetidae and Blochiidae

can be readily explained as the result of competitive replacement by the modern xiphioid billfishes. Except for these six taxa, the complexion of the North Atlantic actinopterygian fish fauna has changed little at the family level since the early Eocene, even though large changes have occurred in world climate since that time. In contrast, nearly all early Eocene birds and mammals belong to extinct families and genera. This striking difference between land and marine vertebrates strongly suggests that the shallow marine environment of the North Atlantic ocean basin has been much less stressed since the early Eocene than the terrestrial environments adjacent to the North Atlantic.

**Table 5. Evolutionary change among the bony fishes from the Fisher/Sullivan site**

	Family Extant	Genus Extant	Both Extinct
<i>Acipenser</i> sp.	X	X	
<i>Lepisosteus</i> sp.	X	X	
<i>Pycnodus</i> sp.			X
<i>Amia</i> sp.	X	X	
<i>Brychaetus muelleri</i>	X		
Megalopidae, gen. et sp. indet.	X		
<i>Albula oweni</i>	X	X	
<i>Albula eppi</i>	X	X	
<i>Egertonia isodonta</i>			X
<i>Phyllodus toliapicus</i>			X
<i>Paralbula marylandica</i>			X
<i>Voltaconger latispinus</i>	X		
cf. <i>Bolcyrus formosissimus</i>	X		
? <i>Arius</i> sp.	X	X	
<i>Cylindracanthus rectus</i>			X
<i>Cyclopoma folmeri</i>	X		
<i>Prolates dormaalensis</i>	X		
cf. <i>Sciaenurus bowerbanki</i>	X		
<i>Fisherichthys folmeri</i>	?		
<i>Sphyræna bagnorensis</i>	X	X	
<i>Trichiurides sagittidens</i>	X		
<i>Teratichthys antiquitatus</i>	X		
<i>Sullivanichthys mccloskeyi</i>	X		
<i>Acanthocybium proosti</i>	X	X	
<i>Sarda delheidi</i>	X	X	
<i>Scomberomorus bleekeri</i>	X	X	
<i>Scomberomorus stormsi</i>	X	X	
<i>Scombrinus</i> sp.	X		
<i>Aglyptorhynchus veneblesi</i>			X
Percomorph A			
Percomorph B			
Percomorph C			
Percomorph D			
Percomorph E			
Percomorph F			
Percomorph G			
Percomorph H			
Percomorph I			
Ostraciidae, gen. et sp. indet.	X		
<b>Totals</b>	<b>24</b>	<b>11</b>	<b>6</b>

**Table 4. Other occurrences of the bony fishes from the Fisher/Sullivan site**

	Gulf Coast	Europe	Africa	India
<i>Acipenser</i> sp.		X		
<i>Lepisosteus</i> sp.	X	X		X
<i>Pycnodus</i> sp.	X	X	X	X
<i>Amia</i> sp.	X	X		
<i>Brychaetus muelleri</i>	X	X	X	
Megalopidae, gen. et sp. indet.		X		
<i>Albula oweni</i>	X	X	X	
<i>Albula eppi</i>		X		
<i>Egertonia isodonta</i>	X	X		
<i>Phyllodus toliapicus</i>	X	X		
<i>Paralbula marylandica</i>				
<i>Voltaconger latispinus</i>		X		
cf. <i>Bolcyrus formosissimus</i>		X		
? <i>Arius</i> sp.		X		
<i>Cylindracanthus rectus</i>		X	X	
<i>Cyclopoma folmeri</i>		X		
<i>Prolates dormaalensis</i>		X		
cf. <i>Sciaenurus bowerbanki</i>		X		
<i>Fisherichthys folmeri</i>	X			
<i>Sphyræna bagnorensis</i>		X		
<i>Trichiurides sagittidens</i>		X		
<i>Teratichthys antiquitatus</i>		X		
<i>Sullivanichthys mccloskeyi</i>				
<i>Acanthocybium proosti</i>		X		
<i>Sarda delheidi</i>		X		
<i>Scomberomorus bleekeri</i>		X		
<i>Scomberomorus stormsi</i>		X		
<i>Scombrinus</i> sp.		X		
<i>Aglyptorhynchus veneblesi</i>		X		
Percomorph A				
Percomorph B				
Percomorph C				
Percomorph D				
Percomorph E				
Percomorph F				
Percomorph G				
Percomorph H				
Percomorph I				
Ostraciidae, gen. et sp. indet.		X	X	X
<b>Totals</b>	<b>8</b>	<b>27</b>	<b>5</b>	<b>3</b>

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## BIBLIOGRAPHY

- Agassiz, Louis, 1833-1844, *Reserches sur les Poissons fossiles*: 5 volumes with atlas, Neuchâtel.
- Agassiz, Louis, 1845, Report on the fossil fishes of the London Clay: Rep. Brit. Ass., London 1844:279-310.
- Arambourg, Camille, 1952, Les Vêrtebrés fossiles des gisements de phosphates (Maroc-Algérie-Tunisie): Notes et Mémoires du Service des Mines et de la Carte géologique du Maroc, 92:1-372.
- Berra, T.M., 1981, An atlas of distribution of the freshwater fish families of the world: University of Nebraska Press, Lincoln, 197 p.
- Blot, Jacques, 1978, Les Apodes Fossiles du Monte Bolca, I: Studi e Ricerche sui Giacimenti Terziari di Bolca (Verona) 3(1):1-260.
- Blot, Jacques, 1987, L'Ordre des Pycnodontiformes, V: Studie Ricerche sui Giacimenti Terziari di Bolca (Verona) 5:1-211.
- Boreske, J.R., Jr., 1974, A review of the North American fossil amiid fishes: Bulletin of the Museum of Comparative Zoology, Harvard University 146(1):1-87.
- Case, G.R., 1986, The bony fishes (teleosts) of the Tusahoma and Bashi formations, early Eocene, Meridian, Lauderdale County, Mississippi: Mississippi Geology, 6(4):6-8.
- Case, G.R., 1994, Fossil fish remains from the Late Paleocene Tusahoma and Early Eocene Bashi Formations of Meridian, Lauderdale County, Mississippi. Part II. Teleosteans: Palaeontographica Abt. A, band 230, lfg. 6, p. 139-153.
- Casier, Edgard, 1946, La faune ichthyologique de l'Yprésien de la Belgique: Mémoires du Musée Royal d'Histoire Naturelle de Belgique, 104:1-267.
- Casier, Edgard, 1959, Contribution à l'étude des poissons fossiles des Antilles: Schweiz. Paläontol. Ges. 74:1-95.
- Casier, Edgard, 1966, Faune Ichthyologique du London Clay, text and atlas: British Museum (Natural History), London, p. 1-496, pl. 1-68.
- Casier, Edgard, 1967, Le Landénien de Dormaal (Brabant) et sa faune ichthyologique: Institut Royal des Sciences Naturelles de Belgique, Mémoire 156:1-65, 8 pl.
- Chalifa, Yael, 1989, Two new species of longirostrine fishes from the early Cenomanian (Late Cretaceous) of Ein-Yabrud, Israel, with comments on the phylogeny of the Dercetidae: Journal of Vertebrate Paleontology, 9(3):314-328.
- Collette, B.B., and Chao, L.N., 1975, Systematics and morphology of the bonitos (*Sarda*) and their relatives (Scombridae, Sardini): U.S. Fish and Wildlife Service Fishery Bulletin 73(3):516-625.
- Collette, B.B., and Russo, J.L., 1984, Morphology, systematics, and biology of Spanish mackerels (*Scomberomorus*, Scombridae): U.S. Fish and Wildlife Service Fishery Bulletin 82(4):545-692.
- Cvancara, A.M., and Hoganson, J.W., 1993, Vertebrates of the Cannonball Formation (Paleocene) in North and South Dakota: Journal of Vertebrate Paleontology 13(1):1-23.
- Dartevelle, E., and Casier, Edgard, 1943, Les poissons fossiles du Bas-Congo et de régions voisines (Première Partie): Ann. Mus. Congo Belge, Ser. A, v. 2, p. 1-200.
- Dartevelle, E., and Casier, Edgard, 1949, Les poissons fossiles du Bas-Congo et de régions voisines (Deuxième Partie): Ann. Mus. Congo Belge, Ser. A, v. 2, p. 201-259.
- Estes, Richard, 1969, Studies on fossil phylloodont fishes: Interrelationships and evolution in the Phylloodontidae (Albuloidae): Copeia 1969(2):317-331.
- Estes, Richard, 1976, Middle Paleocene lower vertebrates from the Tongue River Formation, southeastern Montana: Journal of Paleontology 50(3):500-520.
- Fallow, W., 1964, *Cylindracanthus* from the Eocene of the Carolinas: Journal of Paleontology 38(1):128-129.
- Forey, P.L., 1973, A revision of the Elopiform fishes, fossil and recent: Bulletin of the British Museum (Natural History), Geology Series, Supplement 10, p. 1-222.
- Frickhinger, K.A., 1995, Fossil Atlas -- Fishes: Singapore, Mergus Press, 1088 p.
- Frigo, M.S., and Sorbini, Lorenzo, 1975, Revisione del genere fossile *Cyclopoma* Agassiz e suoi rapporti con l'attuale genere *Perkalates* Ramsey e Ogilby (Pisces): Studi e Ricerche sui Giacimenti Terziari di Bolca (Verona) 2(2):55-102.
- Gayet, Mireille, Rage, J.-C., and Rana, R.S., 1984, Nouvelle ichthyofaune et herpetofaune de Gitti Khada, le plus ancien gisement connu du Déccan (Crétacé/Paléocène) à microvertèbres. Implications paléogéographiques: Mémoires de la Société géologique de France, nouvelle série, 147:55-65.
- Gildersleeve, Benjamin, 1933, Pharyngeal plates of *Phyllodus* from the Virginia Eocene: Journal of the Washington Academy of Science 23:380-389.
- Goody, P.C., 1969, The relationships of certain Upper Cretaceous teleosts with special reference to the myctophoids: Bulletin of the British Museum (Natural History), Geology 7:1-255.
- Grande, Lance, 1980, Paleontology of the Green River Formation, with a review of the fish fauna: Wyoming Geological Survey Bulletin 63:1-333.
- Gregory, W.K., 1933, Fish skulls: A study of the evolution of

natural mechanisms: Transactions of the American Philosophical Society 23(2):1-481.

Gregory, W.K., 1951, Evolution emerging: New York, 2 volumes (text and atlas), 1013 pp.

Herman, J., 1972, Contribution a la connaissance de la faune ichthyologique de phosphates du Maroc: Ann. Soc. Géol. Belg. 95(2):271-283.

Hopkins, F.V., 1870, First annual report of the Louisiana State Geological Survey: Annual Report, Board of Supervisors, Louisiana State Seminary of Learning and Military Academy for the year ending December 31, 1869, Session of 1870, p. 77-109.

Kemp, David, Kemp, Liz, and Ward, David, 1990, An illustrated guide to the British middle Eocene vertebrates: David Ward, London, 59 p.

Kumar, Kishor, and Loyal, R.S., 1987, Eocene ichthyofauna from the Subathu Formation, northwestern Himalaya, India: Journal of the Palaeontological Society of India 32:60-84.

Leriche, Maurice, 1900, Sur la Faune ichthyologique des Sables à Unios et Térédines des Environs d'Épernay (Marne): Annales de la Société Géologique du Nord, 29:173-196.

Leriche, Maurice, 1902, Les Poissons paléocènes de la Belgique: Mémoires du Musée Royal d'Histoire Naturelle de Belgique, 2:1-48.

Leriche, Maurice, 1905, Les Poissons éocènes de la Belgique: Mémoires du Musée Royal d'Histoire Naturelle de Belgique, (Brussels), 3:49-228.

Leriche, Maurice, 1906, Contribution à l'étude des Poissons fossiles du Nord de la France et des régions voisines: Mémoires de la Société Géologique du Nord (Lille), 5:1-430.

Leriche, Maurice, 1923, Les Poissons paléocènes et éocènes du Bassin de Paris (note additionnelle): Bulletin de la Société Géologique de France, Ser. 4, 22(6-7):177-200.

Leriche, Maurice, 1942, Contribution à l'étude faunes ichthyologiques marines des terrains tertiaires de la plaine côtière Atlantique et du centre des États-Unis. Le synchronisme des formations tertiaires des deux côtés de l'Atlantique: Mémoires de la Société Géologique de France (Paris), n.s., 20(2-4):1-111.

Longbottom, A.E., 1984, New Tertiary pycnodonts from the Tilemsi valley, Republic of Mali: Bulletin of the British Museum (Natural History), Geology Series 38(1):1-26.

Lucas, S.G., 1984, Early Paleocene vertebrates, stratigraphy and biostratigraphy, West Fork of Gallegos Canyon, San Juan Basin, New Mexico: New Mexico Geology 6(3):56-60.

Luundberg, J. G., 1975, The fossil catfishes of North America: University of Michigan Papers on paleontology 11:1-51.

Nakamura, I., and Parin, N.V., 1993, Snake Mackerels and cutlassfishes of the world: Food and Agricultural Organization Species Catalogue, 15(125):1-53.

Schultz, Ortwin, 1987, Taxonomische Neugruppierung der

überfamilie Xiphoidea (Pisces, Osteichthyes): Annalen des Naturhistorischen Museums in Wien, ser. A, 89:95-202.

Storms, Raymond, 1892, Sur le *Cybium* (*Enchodus*) *bleekeri* du terrain bruxellien: Mémoires de la Société Belge, de Géologie, de Paléontologie et d'Hydrologie, 6:3-14.

Storms, Raymond, 1897, Un nouveau *Cybium* du terrain bruxellien: Rev. Quest. Sci. (Brussels), ser. 2, 12:242-247.

Taverne, Louis, 1977, Ostéologie, phylogénèse et systématique des Téléostéens fossiles et actuels du super-ordre des Ostéoglossomorphes; Première partie, Ostéologie des genres *Hiodon*, *Eohiodon*, *Lycoptera*, *Osteoglossum*, *Scleropages*, *Heterotis*, et *Arapaima*: Académie Royale de Belgique, Mémoires de la Classe des Sciences, Series 2, 42(3):1-235.

Taverne, Louis, 1978, Ostéologie, phylogénèse et systématique des Téléostéens fossiles et actuels du super-ordre des Ostéoglossomorphes; Deuxième partie, Ostéologie des genres *Phareodus*, *Brychaetus*, *Musperia*, *Pantodon*, *Singida*, *Notopterus*, *Xenomystus*, et *Papyrocranus*: Académie Royale de Belgique, Mémoires de la Classe des Sciences, Series 2, 42(6):1-213.

Thurmond, J.T., and Jones, D.E., 1981, Fossil vertebrates of Alabama: University of Alabama Press, University of Alabama, 244 p.

Tyler, J.C., 1975, A new species of boxfish from the Eocene of Monte Bolca, Italy; the first unquestionable fossil record of the Ostraciontidae: Studi e Ricerche sui Giacimenti Terziari di Bolca (Verona), 2(3):103-126.

Tyler, J.C., 1980, Osteology, phylogeny, and higher classification of the fishes of the Order Plectognathi (Tetraodontiformes): Department of Commerce, NOAA Technical Report, NMFS Circular 434, 422 pp.

Tyler, J.C., and Gregorova, R., 1991, A new genus and species of boxfish (Tetraodontiformes: Ostraciidae) from the Oligocene of Moravia, the second fossil representative of the family: Smithsonian Contributions to Paleobiology, 71:1-20.

Ward, D.J., 1978, The lower London Tertiary (Palaeocene) succession of Herne Bay, Kent: Institute of Geological Sciences (Natural Environment Research Council) Report 78/10: London, Her Majesty's Stationery Office, 12 pp.

Weems, R.E., 1998, Actinopterygian fish remains from the Paleocene of South Carolina: in Sanders, A.E., editor, Paleobiology of the Williamsburg Formation (Black Mingo Group; Paleocene) of South Carolina (USA): Transactions of the American Philosophical Society, 88(4):147-164.

Weems, R.E., and Horman, S.R., 1983, Teleost fish remains (Osteoglossidae, Blochiidae, Scombridae, Triodontidae, Diodontidae) from the lower Eocene Nanjemoy Formation of Maryland: Proceedings of the Biological Society of Washington 96(1):38-49.

Westgate, J.W., 1984, Lower vertebrates from the late Eocene Crow Creek local fauna, St. Francis County, Arkansas: Journal of Vertebrate Paleontology 4(4):536-546.

Westgate, J.W., 1989, Lower vertebrates from an estuarine facies of the middle Eocene Laredo Formation (Claiborne Group), Webb County, Texas: *Journal of Vertebrate Paleontology* 9(3):282-294.

Wheeler, Alwyne, 1975, *Fishes of the world; an illustrated dictionary*: New York, MacMillan Publishing Company, 366 pp.

White, E.I., 1931, The vertebrate faunas of the English Eocene: Vol. 1. From the Thanet Sands to the Basement Bed of the London Clay: British Museum (Natural History), 123 pp.

White, E.I., 1935, Fossil fishes of Sokoto province: *Bulletin of the Geological Survey of Nigeria*, 14:1-78.

Wiley, E.O., 1976, The phylogeny and biogeography of fossil and recent gars (Actinopterygii: Lepisosteidae): University of Kansas Museum of Natural History, Miscellaneous Publication 64:1-111.

Winkler, T.C., 1874, Deuxième mémoire sur des dents de poissons fossiles du terrain bruxellien: *Archives du Musée Teyler (Haarlem)* 4(1):1-33.

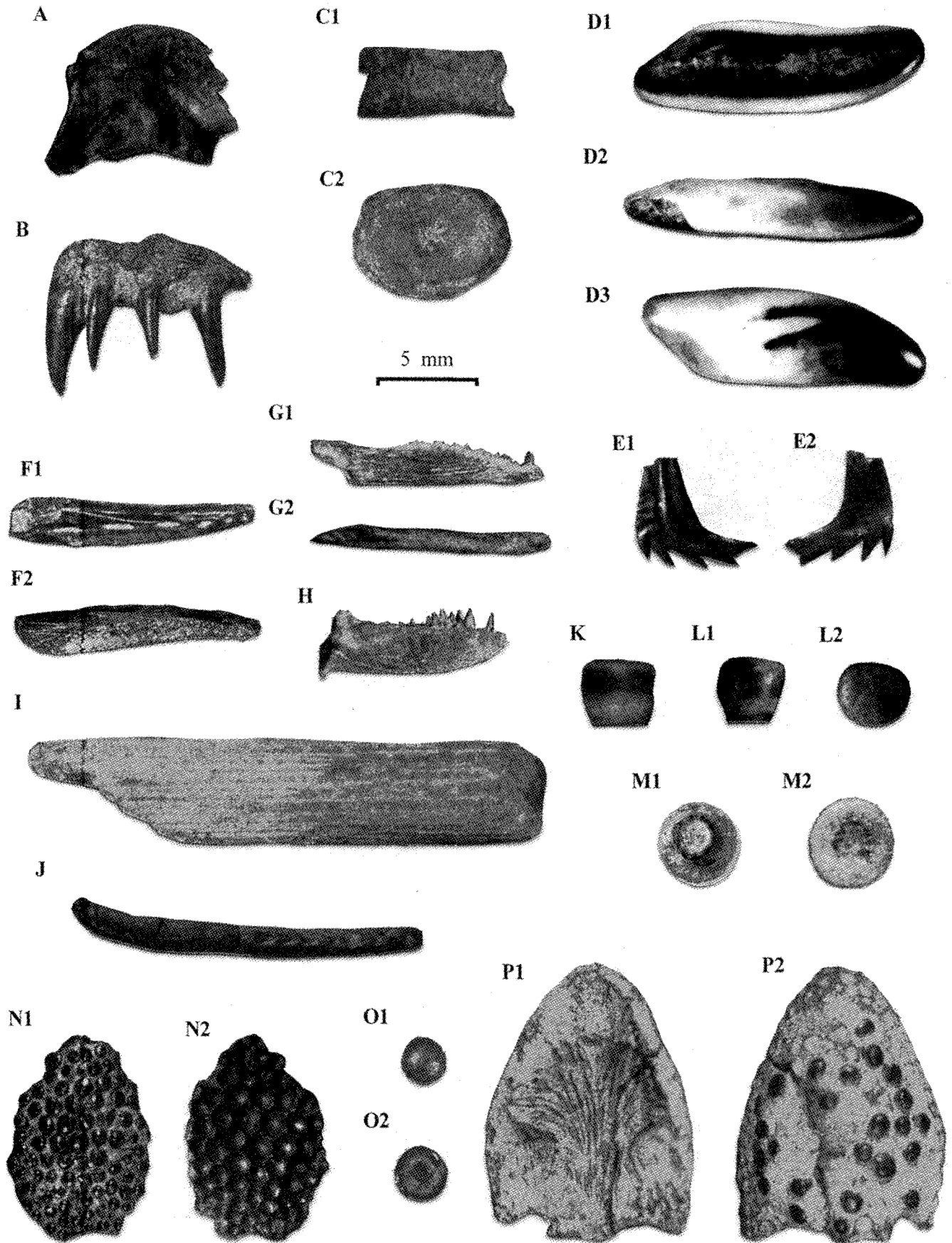
Winterbottom, R., and Tyler, J.C., 1983, Phylogenetic relationships of Aracanin genera of boxfishes (Ostraciidae: Tetraodontiformes): *Copeia* 1983(4):902-917.

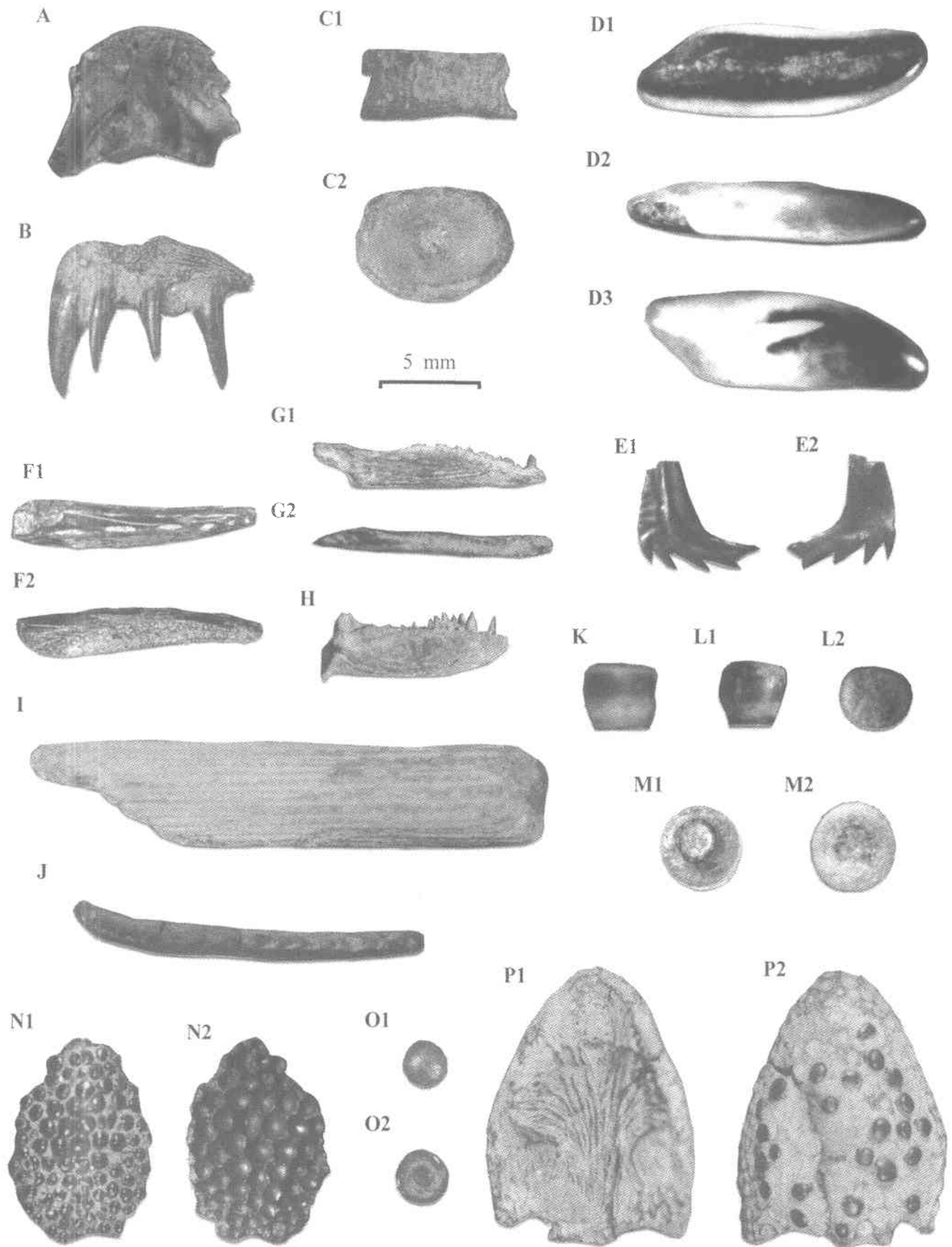
Wood, S.V., 1846, On the discovery of an alligator and of several new Mammalia in the Hordwell Cliff, with observations upon the geological phenomena of that locality: *London Geological Journal* 1:1-7, 117-122.

Woodward, A.S., 1901, Catalogue of the fossil fishes in the British Museum (Natural History): Part IV. Containing the actynopterygian Teleostomi of the suborders Isospondyli (in part), Ostariophysi, Apodes, Percosoces, Hemibranchii, Acanthopterygii, and Anacanthini: London, Taylor and Francis, 636 p., 18 pl.

#### Plate 4.1.

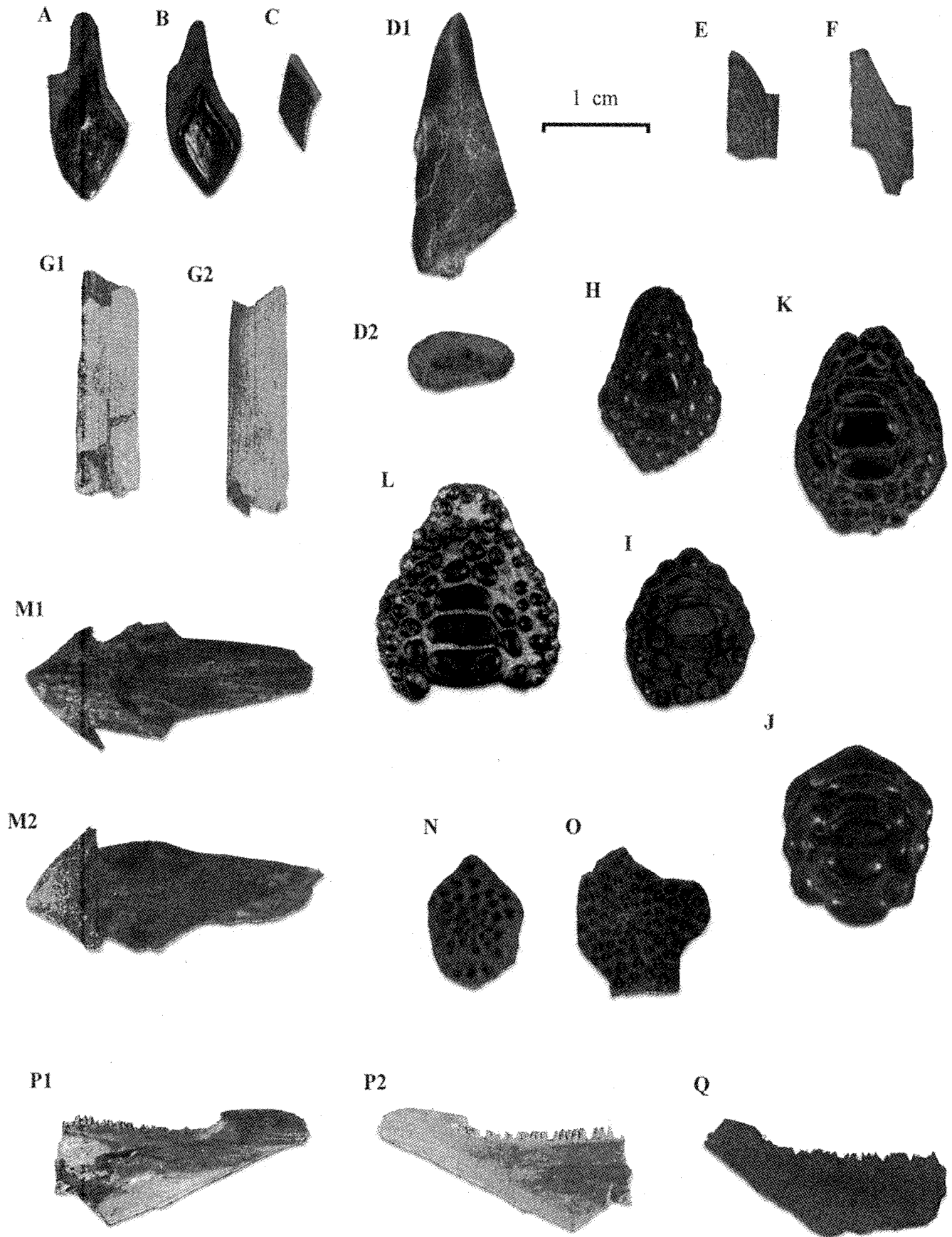
- A. *Lepisosteus* sp., vertebra, Parks collection.
- B. *Amia* sp., premaxillary (USNM 496216), Folmer collection.
- C. *Amia* sp., vertebra (USNM 496217) in dorsal (C1) and anterior (C2) views, Grimsley collection.
- D. *Pycnodus* sp., tooth (USNM 496218) in aboral (D1), lateral (D2), and oral (D3) views, Savia collection.
- E. *Prolates dormaalensis*, ventral half of left preopercular (USNM 482287) in external (E1) and internal (E2) views, Grimsley collection.
- F. cf. *Bolcyrus formosissimus*, dentary fragment (USNM 496220) in lateral (F1) and oral (F2) views, Grimsley collection.
- G. ?*Arius* sp., pectoral spine (USNM 496221) in lateral (G1) and dorsal (G2) views, Cunningham collection.
- H. ?*Arius* sp., pectoral spine (USNM 496222) in lateral view, Ball collection.
- I. *Cylindracanthus rectus*, rostral fragment (USNM 496223), Folmer collection.
- J. *Voltaconger latispinus*, maxillary (USNM 496224) in oral view, Grimsley collection.
- K. *Albula oweni*, tooth (USNM 496225) in lateral view, Ball collection.
- L. *Albula oweni*, tooth (USNM 496226) in lateral (L1) and oral (L2) views, Grimsley collection.
- M. *Albula oweni*, tooth (USNM 496227) in aboral view (M1) and oral (M2) views, Grimsley collection.
- N. *Egertonia isodonta*, pharyngeal plate (USNM 496228) in oral (N1) and aboral (N2) views, Cunningham collection.
- O. *Paralbula marylandica*, tooth (USNM 496229) in oral (O1) and aboral (O2) views, Grimsley collection.
- P. *Albula eppsi*, pharyngeal plate (USNM 496230) in aboral (P1) and oral (P2) views, Keil collection.

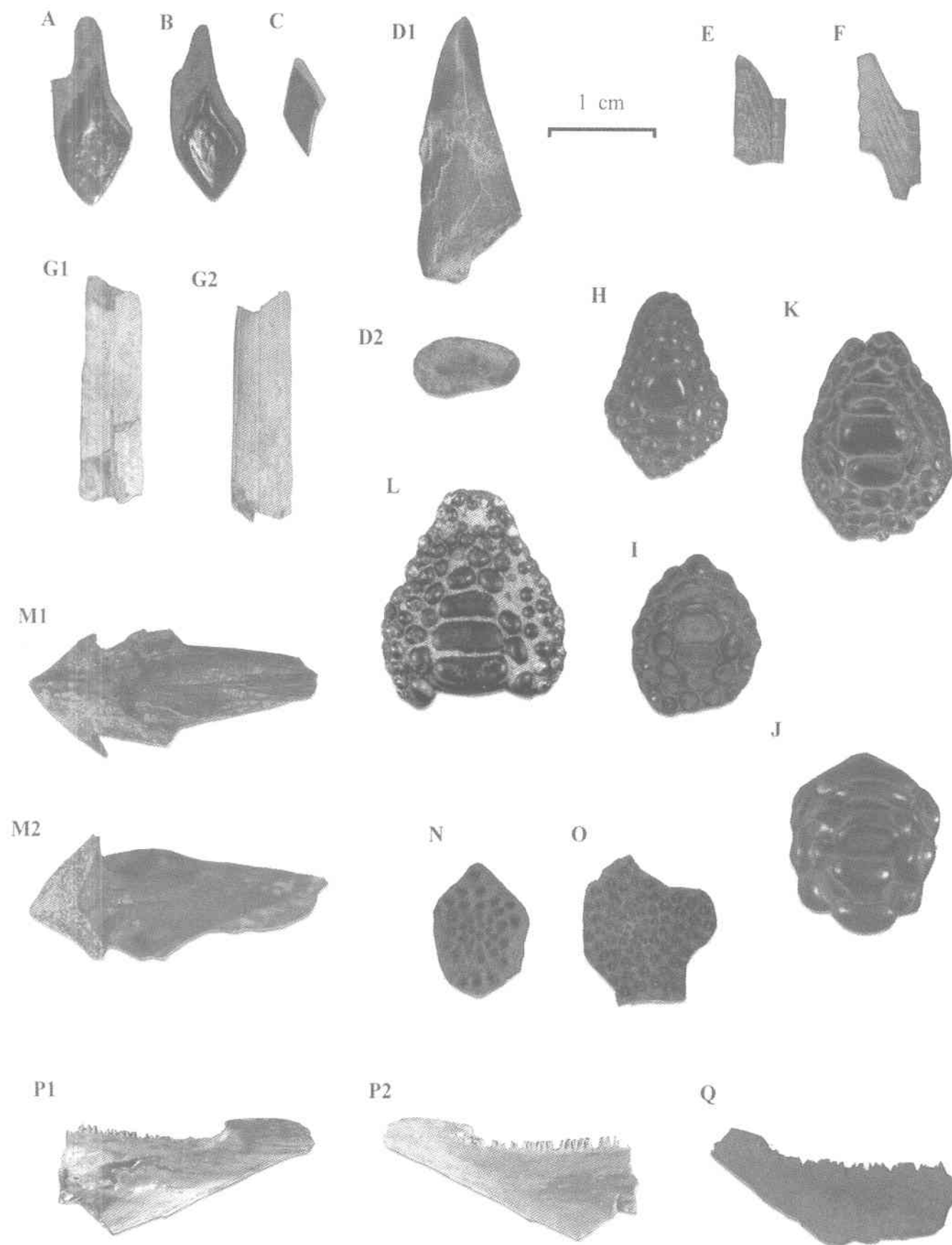




**Plate 4.2.**

- A. *Lepisosteus* sp., scale (USNM 496300) in external view, Ball collection.
- B. *Lepisosteus* sp. scale (USNM 496296) in external view, Folmer collection.
- C. *Lepisosteus* sp. scale (USNM 496298) in external view, Ball collection.
- D. *Brychaetus muelleri*, tooth (USNM 496231) in anterior (D1) and aboral (D2) views, Folmer collection.
- E. Megalopidae, gen. et sp. indet., fin spine fragment (USNM 496232), Folmer collection.
- F. Megalopidae, gen. et sp. indet., fin spine fragment (USNM 496233), Folmer collection.
- G. *Aglyptorhynchus venablesi*, premaxillary beak fragment (USNM 496234), Folmer collection.
- H. *Phyllodus toliapicus*, pharyngeal plate (USNM 496302) in oral view, Folmer collection.
- I. *Phyllodus toliapicus*, pharyngeal plate (USNM 496303) in oral view, Ball collection.
- J. *Phyllodus toliapicus*, pharyngeal plate (USNM 496301) in oral view, Folmer collection.
- K. *Phyllodus toliapicus*, pharyngeal plate (USNM 496304) in oral view, Cunningham collection.
- L. *Phyllodus toliapicus*, pharyngeal plate (USNM 496235) in oral view, Folmer collection.
- M. *Cyclopoma folmeri* sp. nov., vomer (USNM 496236) in dorsal (M1) and ventral (M2) views, Folmer collection.
- N. Ostraciidae, gen. et sp. indet., dermal plate (USNM 496294), Ball collection.
- O. Ostraciidae, gen. et sp. indet., dermal plate (USNM 496292), Folmer collection.
- P. *Voltaconger latispinus*, dentary fragment in internal (P1) and external (P2) views, Parks collection.
- Q. *Voltaconger latispinus*, dentary fragment (USNM 496237) in external view, Folmer collection.

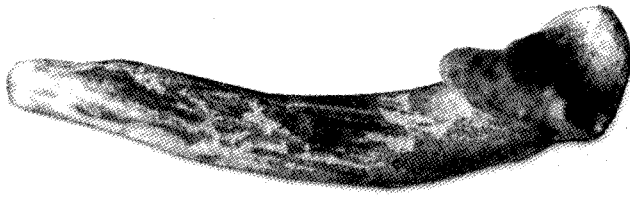




**Plate 4.3.**

- A. *Cyclopoma folmeri* sp. nov., premaxillary (USNM 496238) in dorsal (A1), internal (A2), external (A3), and ventral (A4) views, Folmer collection.
- B. *Acanthocybium proosti*, dentary in internal (B1), external (B2), and dorsal (B3) views, Parks collection.
- C. *Aglyptorhynchus veneblesi*, vertebra (USNM 496239) in lateral view, Folmer collection.
- D. *Aglyptorhynchus veneblesi*, vertebra (USNM 496240) in lateral view, Grimsley collection.
- E. *Aglyptorhynchus veneblesi*, hypural fan in lateral view, Parks collection.
- F. *Aglyptorhynchus veneblesi*, hypural fan (USNM 496241) in lateral view, Harding collection.
- G. *Aglyptorhynchus veneblesi*, premaxillary beak (USNM 496242) in dorsal (top) and ventral (bottom) view, Grimsley collection.

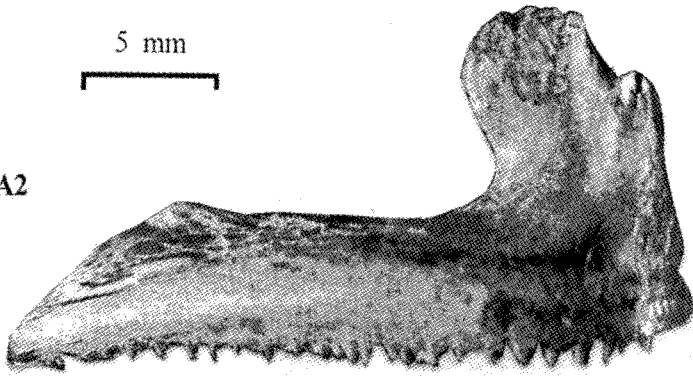
A1



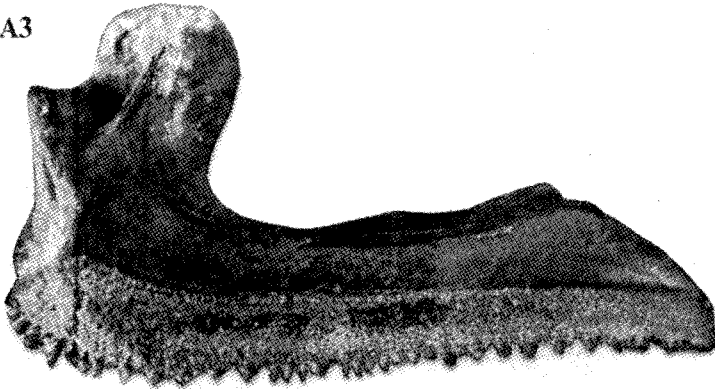
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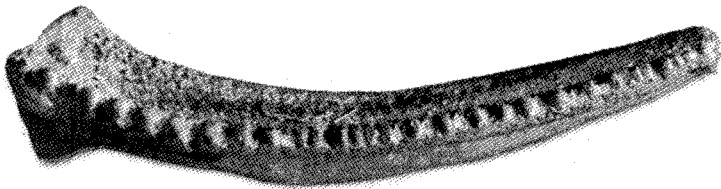
A2



A3



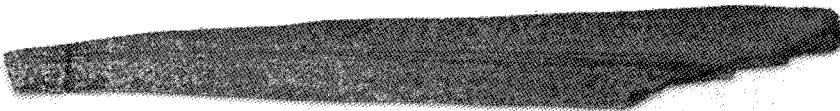
A4



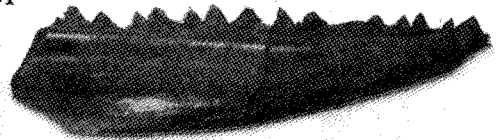
G1



G2



B1



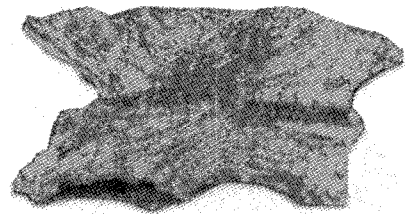
B2



B3



C



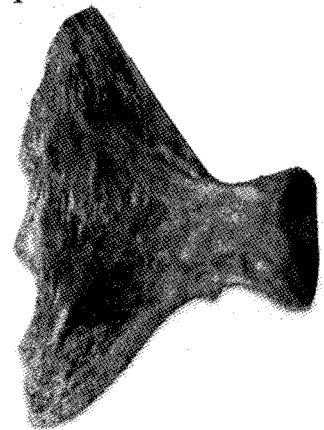
D



E



F



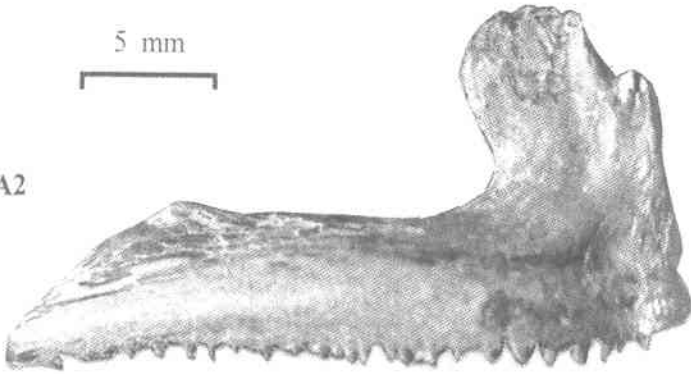
A1



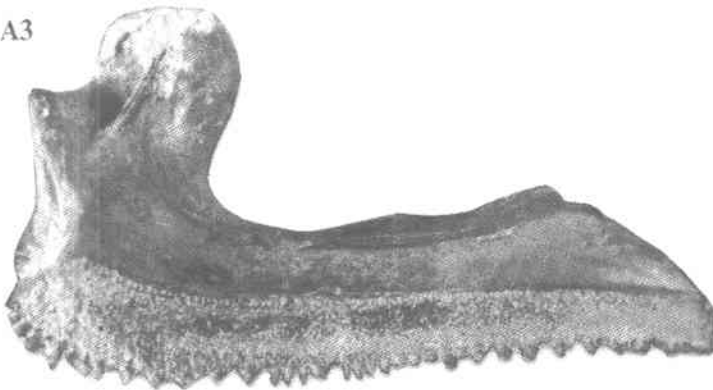
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A2



A3



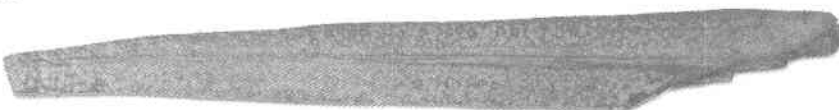
A4



G1



G2



B1



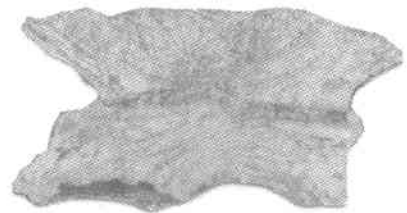
B2



B3



C



D



E



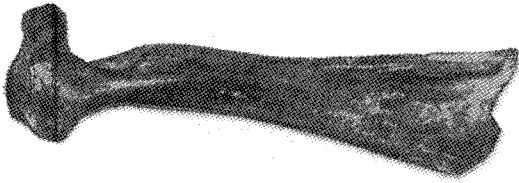
F



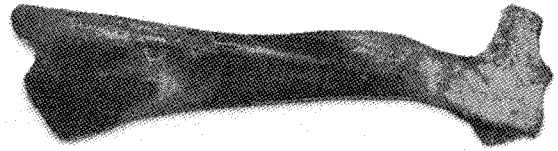
**Plate 4.4.**

- A. *Sullivanichthys mccloskeyi* gen. et sp. nov., right maxillary (USNM 496243) in internal (A1), external (A2), and dorsal (A3) views, Folmer collection.
- B. *Sullivanichthys mccloskeyi* gen. et sp. nov., right dentary (USNM 496244) in oral (B1), internal (B2), and external (B3) views, McCloskey collection.
- C. *Brychaetus muelleri*, premaxillary(?) fragment (USNM 496245) in external (C1) and oral (C2) views, Grier collection.
- D. cf. *Sciaenurus bowerbanki*, anterior portion of right dentary (USNM 496246) in oral (D1), internal (D2), and external (D3) views, McCloskey collection.
- E. Percomorph A, fused pharyngeals with tooth plate (USNM 496247) in oral (E1) and aboral (E2) views, Folmer collection.
- F. Percomorph vertebra (USNM 496248) in anterior (F1) and lateral (F2) views, Savia collection.
- G. Percomorph bony fin spine (USNM 496249) in lateral (G1) and posterior (G2) views, Savia collection.

A1



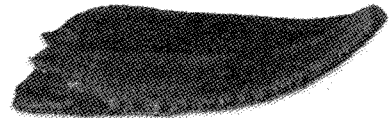
A2



A3



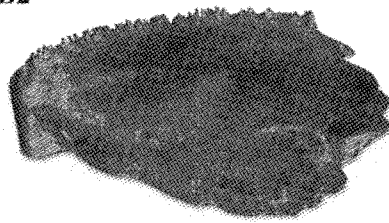
B1



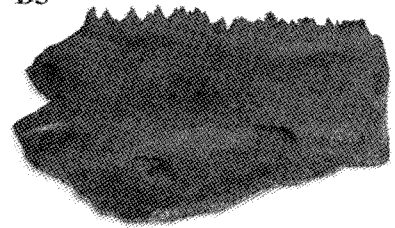
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B2



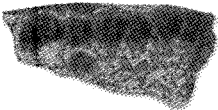
B3



C1



C2



D1



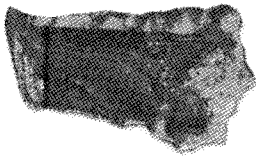
E1



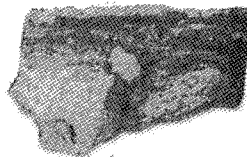
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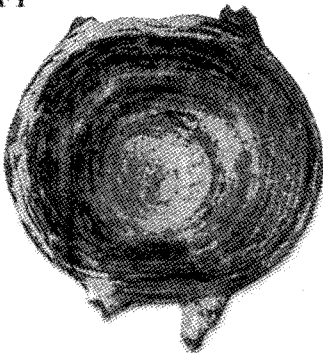
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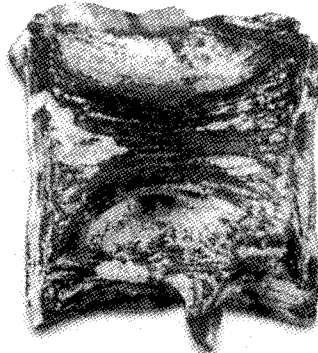
D3



F1



F2



G1



G2



A1



A2



A3



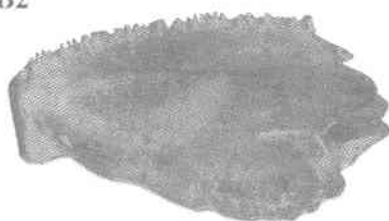
B1



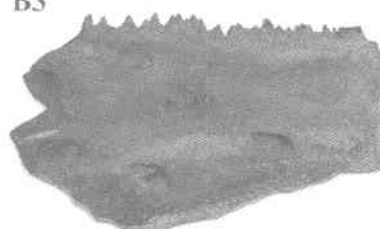
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B2



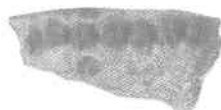
B3



C1



C2



D1



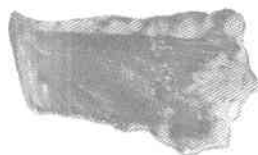
E1



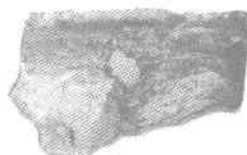
E2



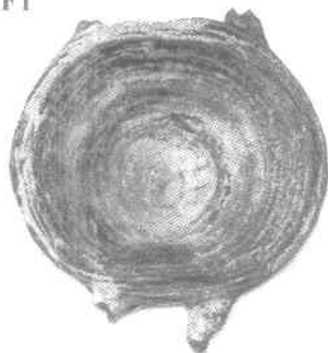
D2



D3



F1



F2



G1

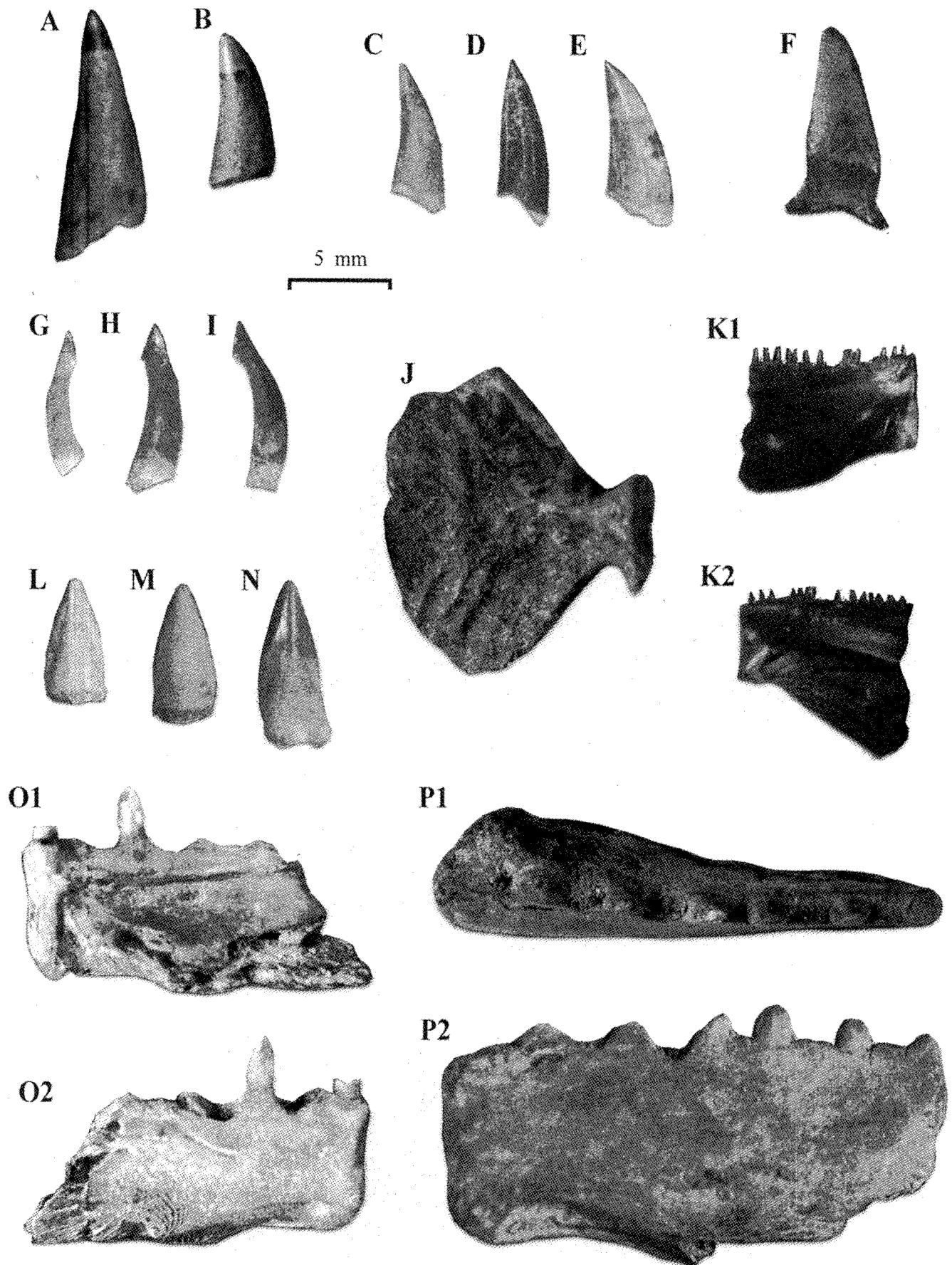


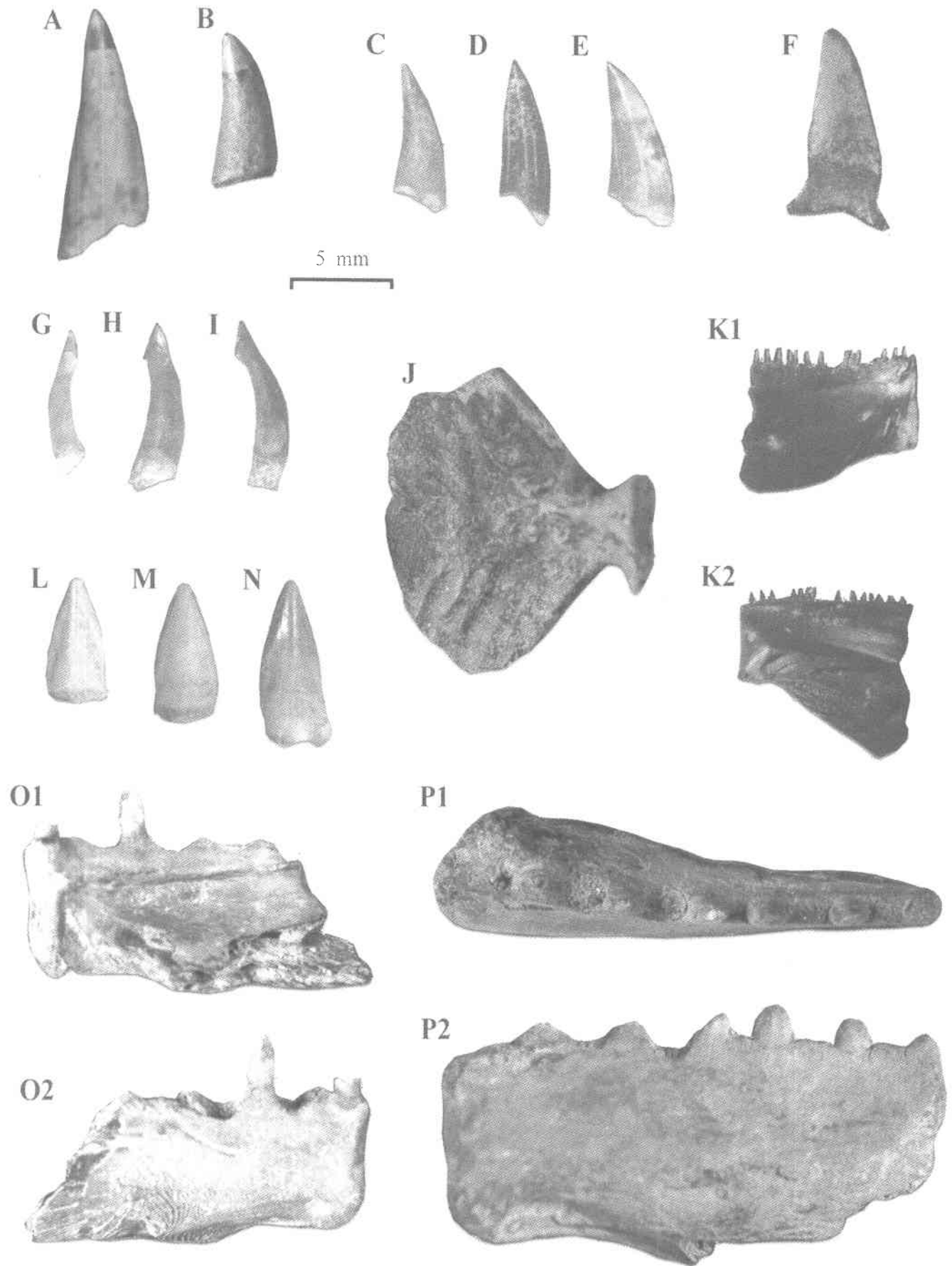
G2



**Plate 4.5.**

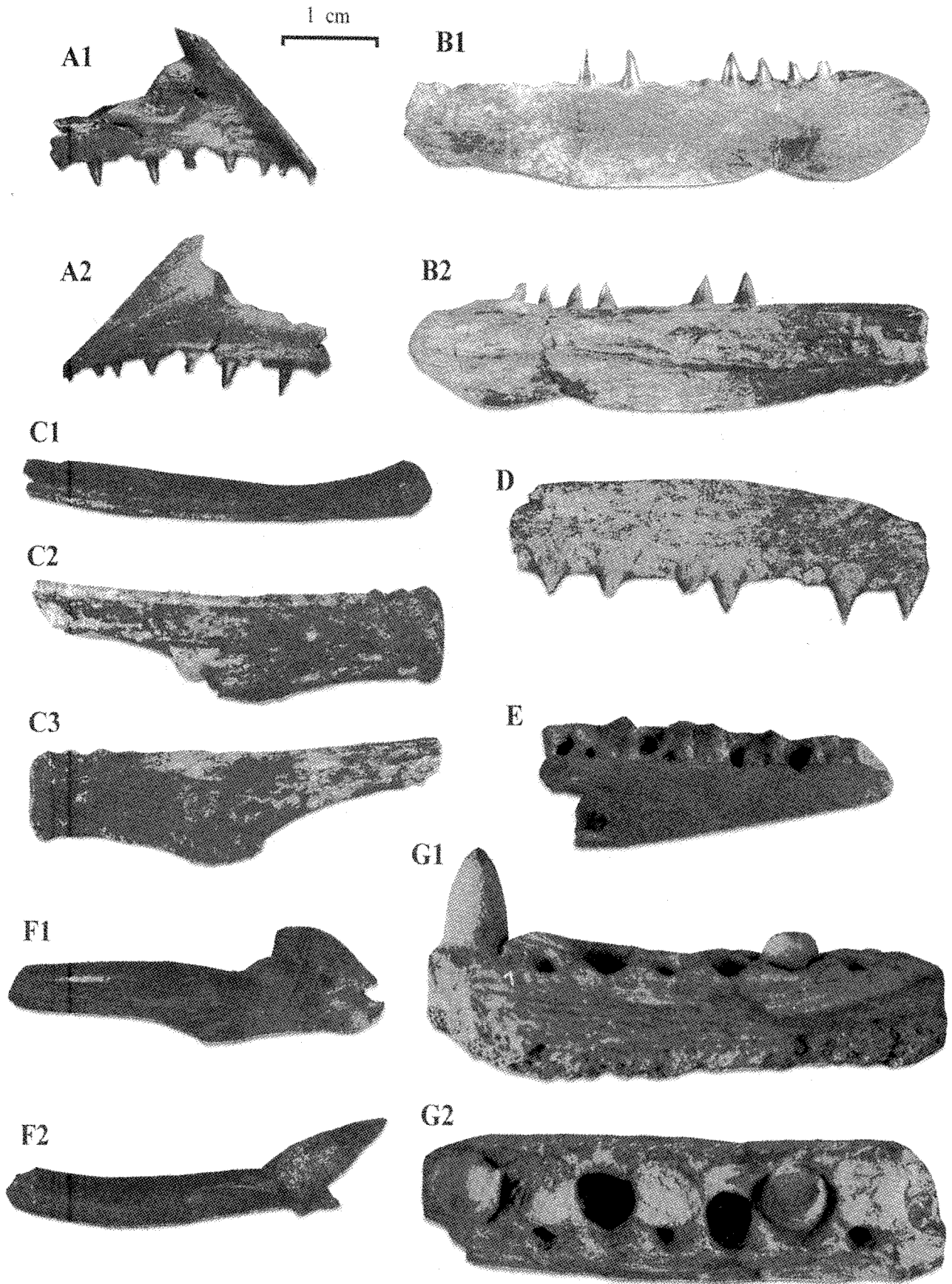
- A. *Brychaetus muelleri*, tooth (USNM 496250), Folmer collection.
- B. *Brychaetus muelleri*, tooth (USNM 496251), Folmer collection.
- C. *Sphyraena bagnorensis*, tooth (USNM 496252), Folmer collection.
- D. *Sphyraena bagnorensis*, tooth (USNM 496253), Folmer collection.
- E. *Sphyraena bagnorensis*, tooth (USNM 496254), Folmer collection.
- F. *Sphyraena bagnorensis*?, tooth (USNM 496255), Folmer collection.
- G. *Trichiurides sagittidens*, tooth (USNM 496256), Folmer collection.
- H. *Trichiurides sagittidens*, tooth (USNM 496257), Folmer collection.
- I. *Trichiurides sagittidens*, tooth (USNM 496258), Folmer collection.
- J. *Scomberomorus* sp., hypural fan (USNM 496259), Harding collection.
- K. *Sullivanichthys mccloskeyi* gen. et sp. nov., anterior portion of dentary (USNM 496260) in internal (K1) and external (K2) view, Ball collection.
- L. *Scomberomorus bleekeri*, tooth (USNM 496261), Grimsley collection.
- M. *Scomberomorus bleekeri*, tooth (USNM 496262), Grimsley collection.
- N. *Scomberomorus bleekeri*, tooth (USNM 496263), Grimsley collection.
- O. *Sarda delheidi*, dentary in internal (O1) and external (O2) view, Savia collection.
- P. *Sarda delheidi*, dentary (USNM 496264) in oral (P1) and external (P2) view, Harding collection.

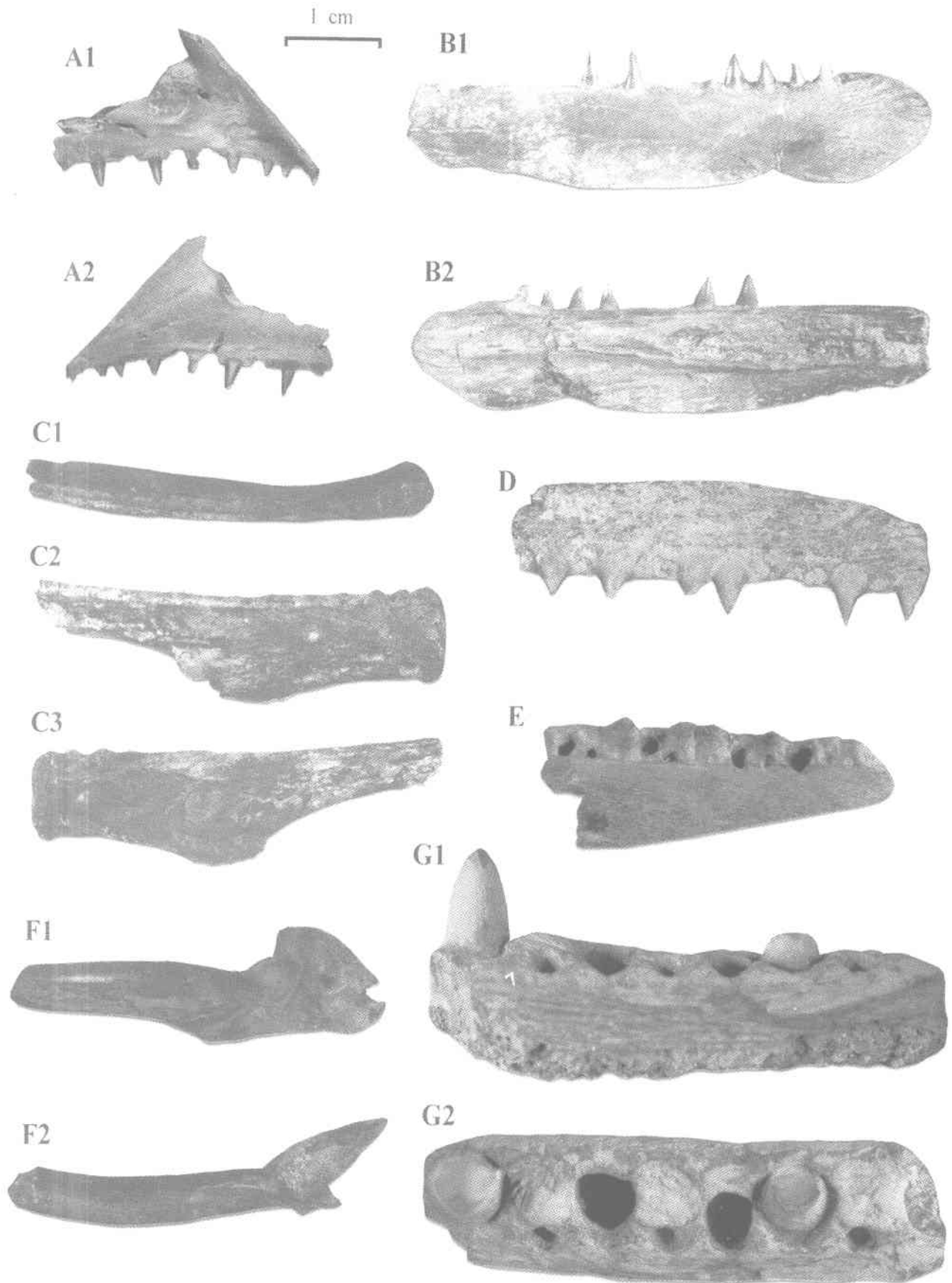




**Plate 4.6.**

- A. *Scomberomorus stormsi*, left premaxillary in internal (A1) and external (A2) views, Parks collection.
- B. *Scomberomorus stormsi*, fragment of left dentary in external (B1) and internal (B2) view, Parks collection.
- C. *Scomberomorus stormsi*, right dentary in oral (C1), external (C2), and internal (C3) views, Parks collection.
- D. *Sarda delheidi*, fragment of premaxillary (USNM 496265) in external view, Ball collection.
- E. *Acanthocybium proosti*, left dentary fragment (USNM 496266) in internal view, Harding collection.
- F. *Scomberomorus* sp., right maxillary in external (F1) and dorsal (F2) views, Parks collection.
- G. *Acanthocybium proosti*, fragment of dentary? (USNM 496267) in lateral (G1) and oral (G2) views, Harding collection.





**Plate 4.7.**

- A. Percomorph B, left premaxillary (USNM 496268) in internal (A1) and external (A2) views, McCloskey collection.
- B. Percomorph B, left premaxillary (USNM 496269) in internal (B1) and external (B2) views, McCloskey collection.
- C. Percomorph C, left premaxillary (USNM 496270) in internal (C1) and external (C2) views, Folmer collection.
- D. *Fisherichthys folmeri* gen. et sp. nov., pharyngeal plate with teeth (USNM 496271) in oral (D1) and lateral (D2) view, Folmer collection.
- E. Ostraciidae, gen. et sp. indet., dermal armor, Ball collection.
- F. Ostraciidae, gen. et sp. indet., dermal armor, Grimsley collection.
- G. Ostraciidae, gen. et sp. indet., dermal armor (USNM 496293), Folmer collection.
- H. *Pycnodus* sp., anterior vomer(?) with teeth and tooth sockets in oral (H1) and aboral (H2) views, Parks collection.

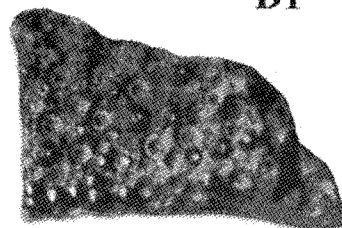
A1



A2



D1



B1



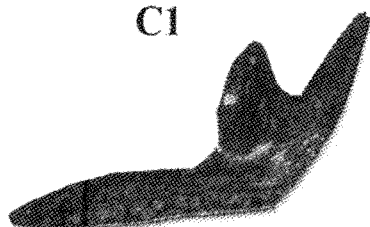
B2



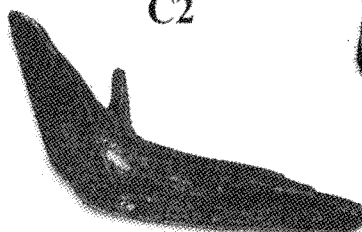
D2



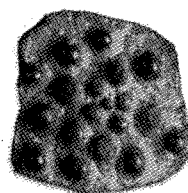
C1



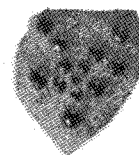
C2



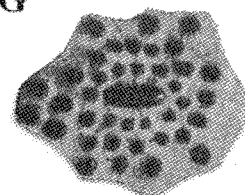
E



F



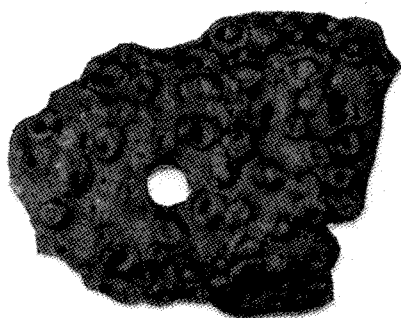
G



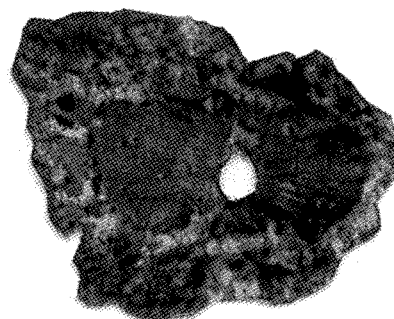
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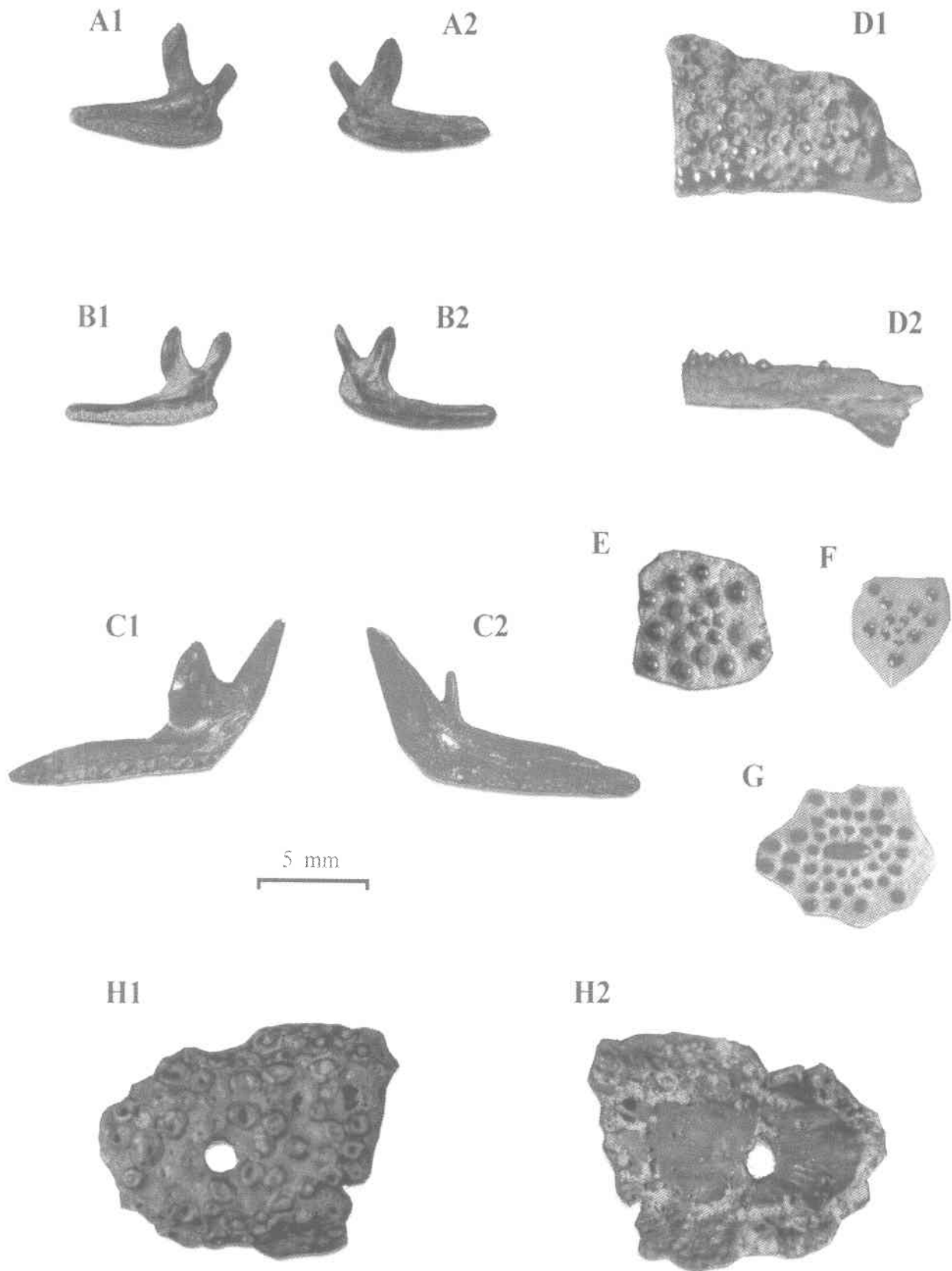


H1



H2

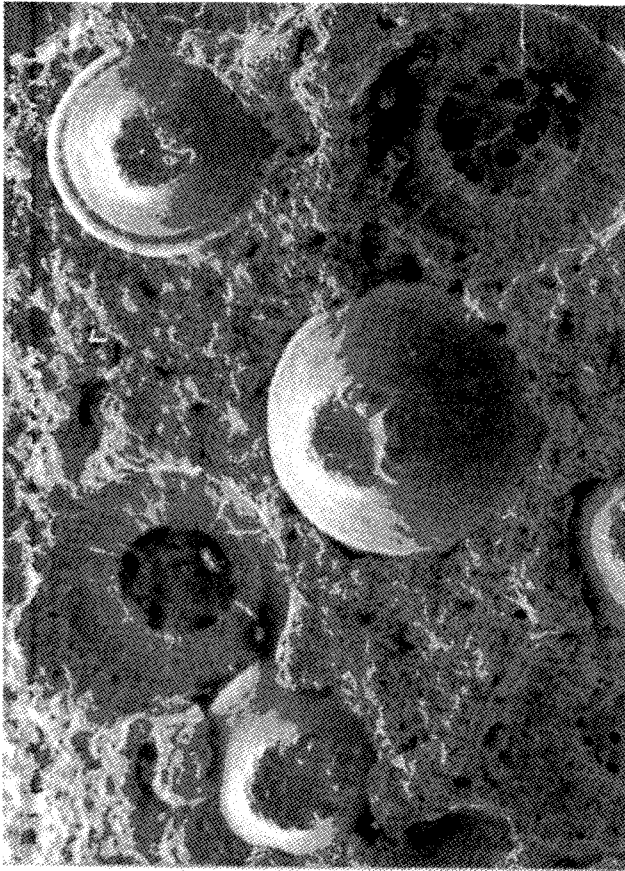




**Plate 4.8.**

- A. Teeth and tooth sockets of *Fisherichthys folmeri* gen. et sp. nov. (USNM 496271), in oral view, Folmer collection.
- B. Teeth and tooth sockets of *Fisherichthys folmeri* gen. et sp. nov. (USNM 496271), in lateral view, Folmer collection.
- C. Anterior dentary teeth (3-6) of *Sullivanichthys mccloskeyi* gen. et sp. nov. (USNM 496244), in oral view, McCloskey collection.
- D. Anterior teeth (3-6, 8, 9, and 11) of *Sullivanichthys mccloskeyi* gen. et sp. nov. (USNM 496244), in lateral view, McCloskey collection.

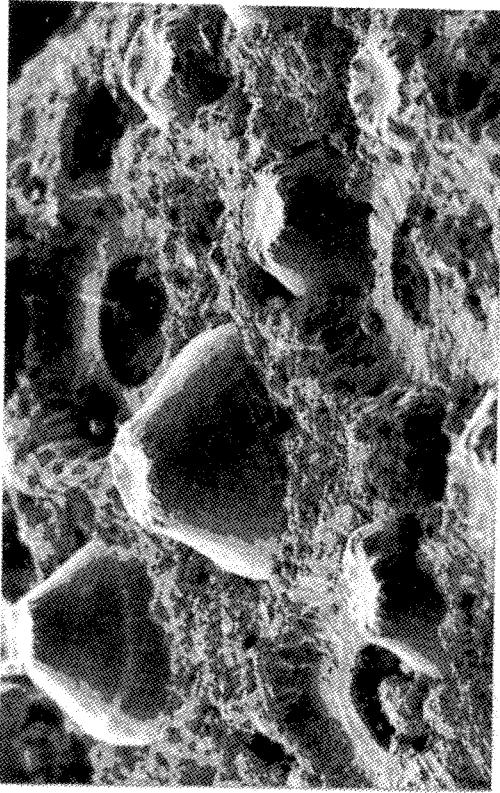
A



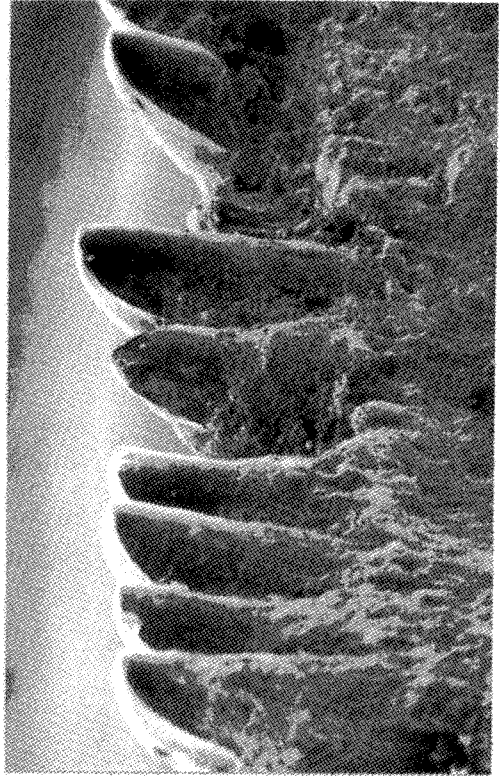
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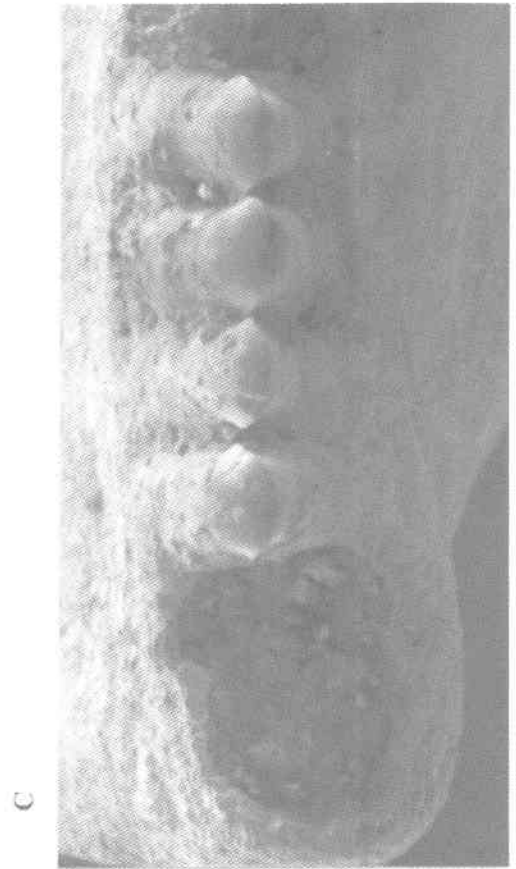
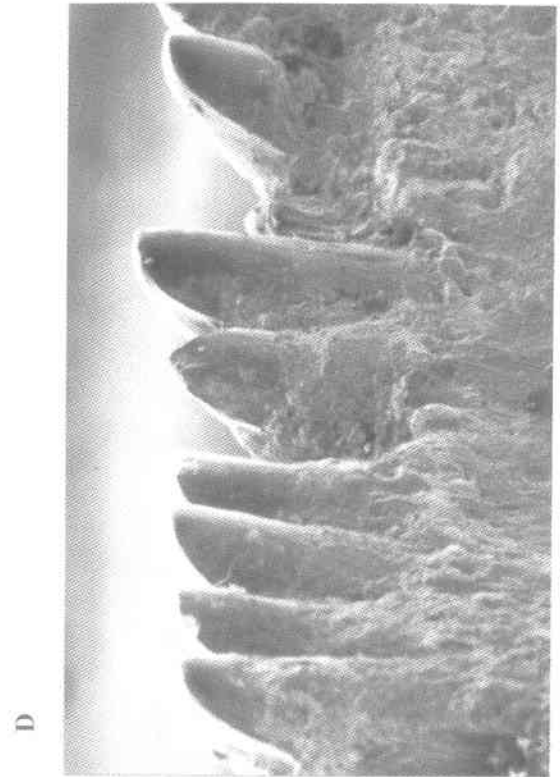
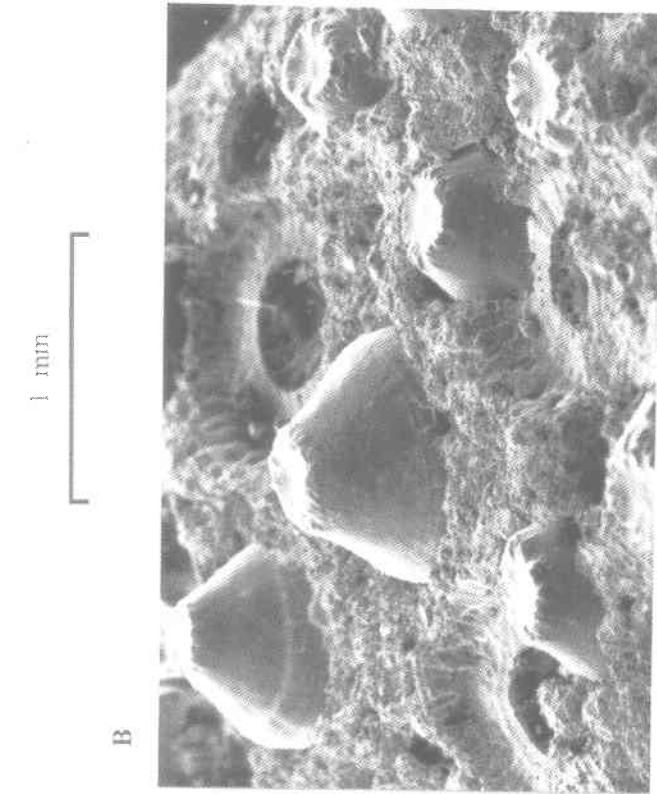


B



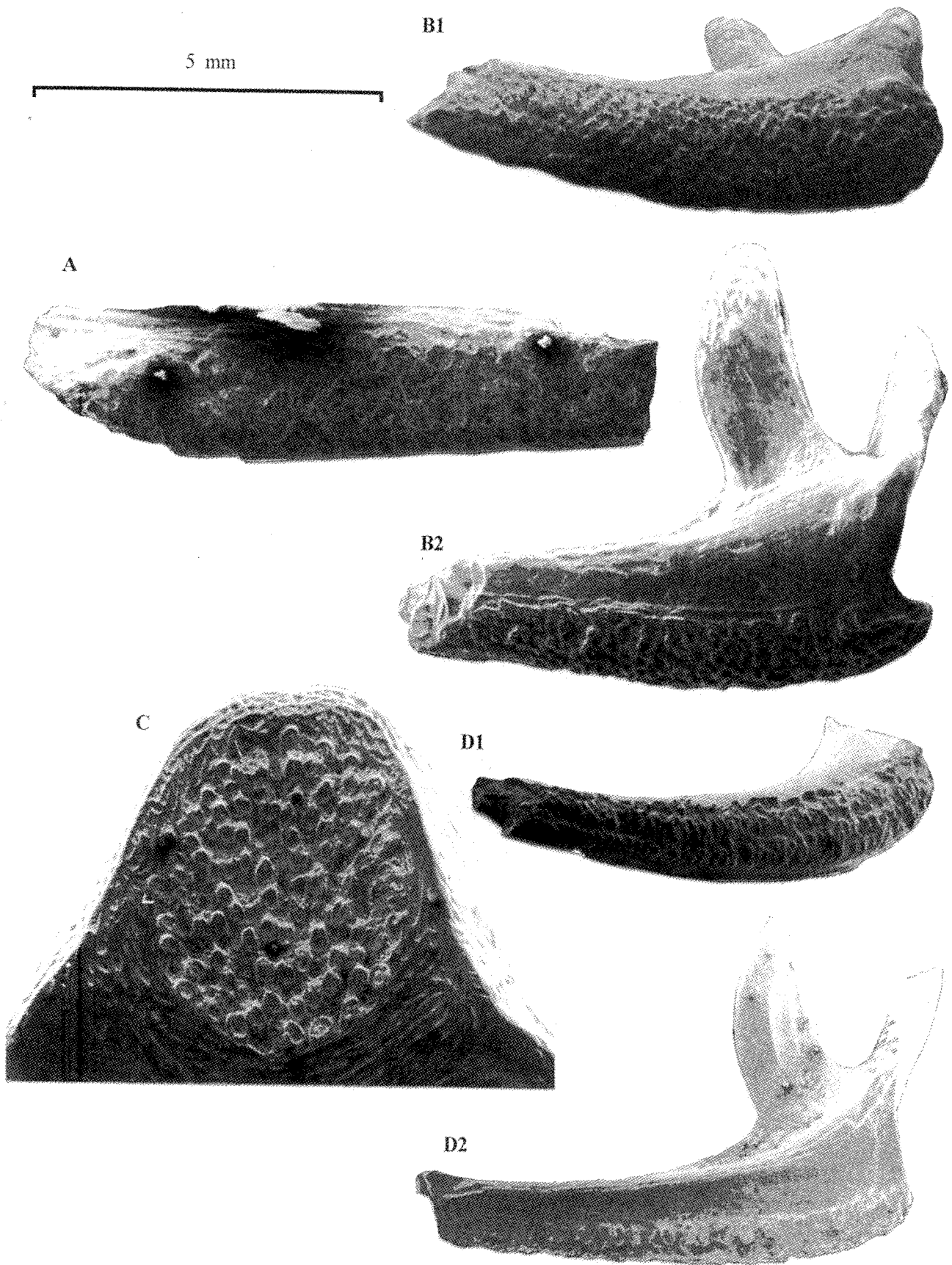
D

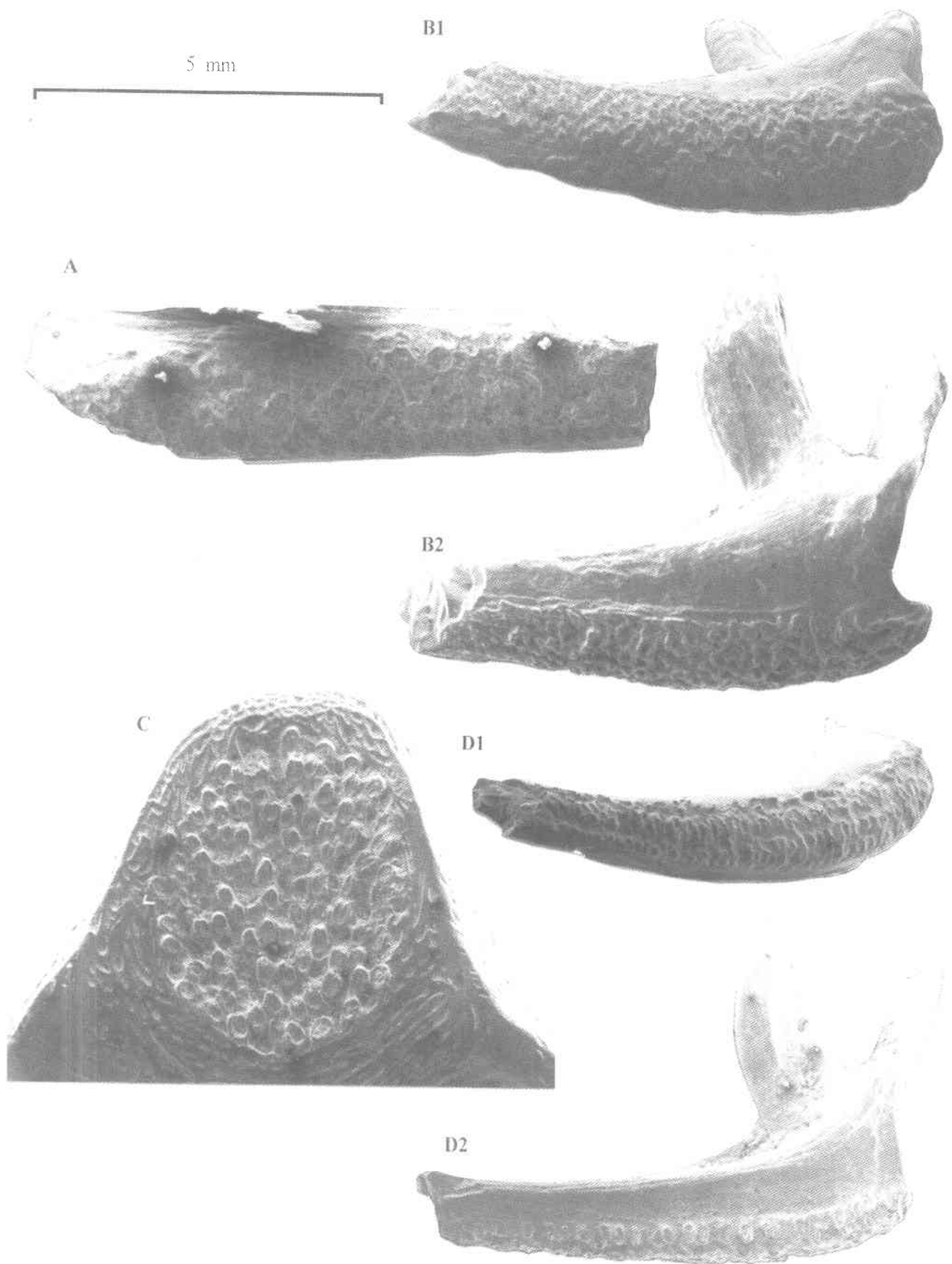




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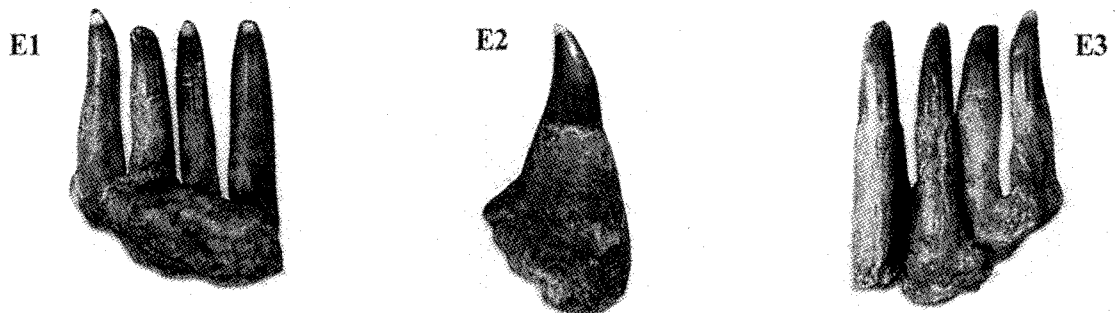
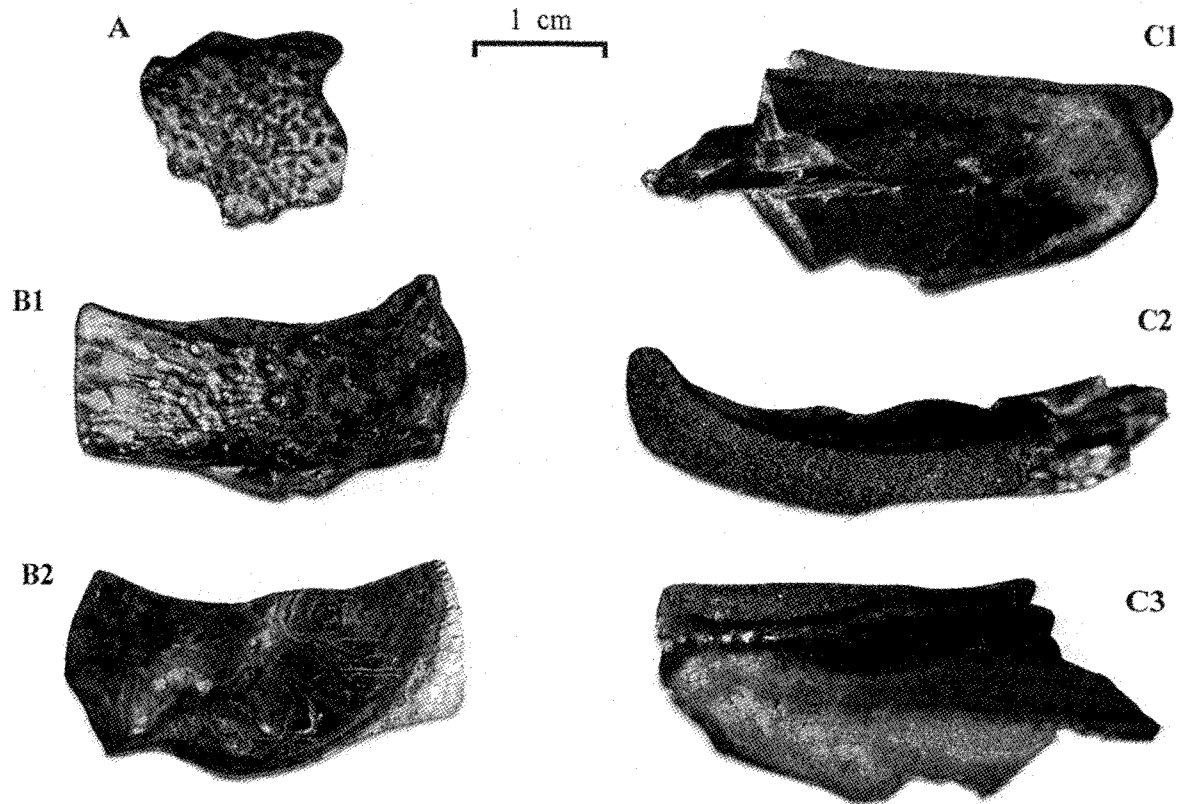
- A. Tooth sockets in dentary of cf. *Bolcyrus formosissimus* (USNM 496220) in oral view, Grimsley collection.
- B. Premaxillary of Percomorph B (USNM 496268) in oral (B1) and internal (B2) views, McCloskey collection.
- C. Tooth sockets in fused pharyngeals of Percomorph A (USNM 496247), Folmer collection.
- D. Premaxillary of Percomorph B (USNM 496269) in oral (D1) and internal (D2) views, McCloskey collection.

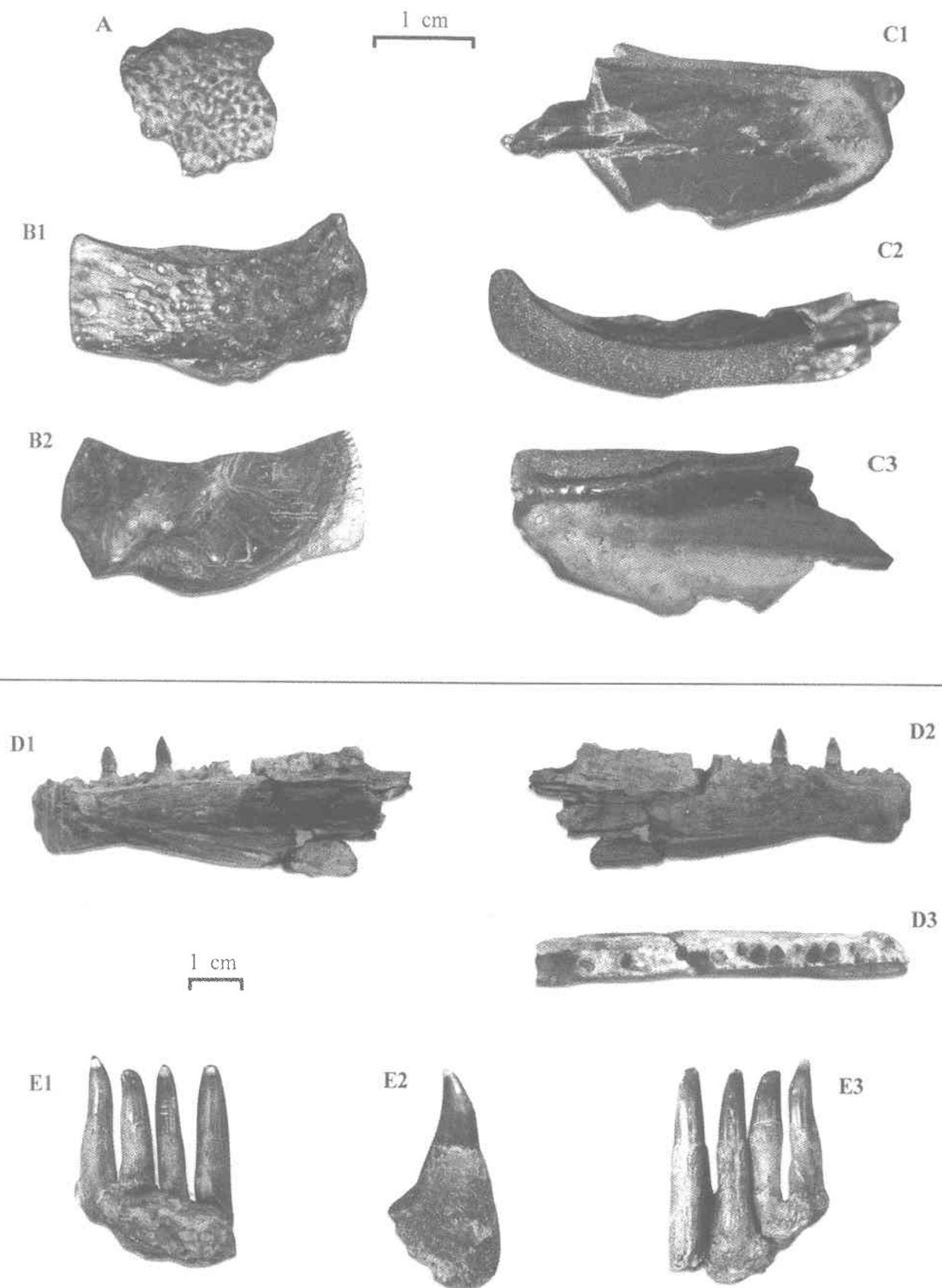




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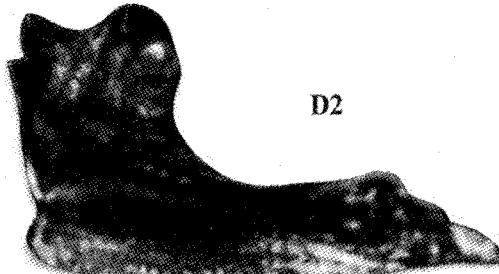
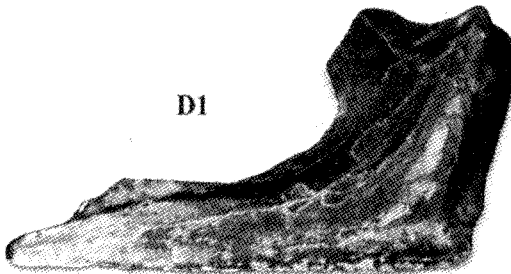
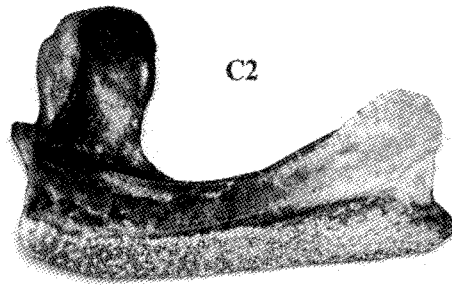
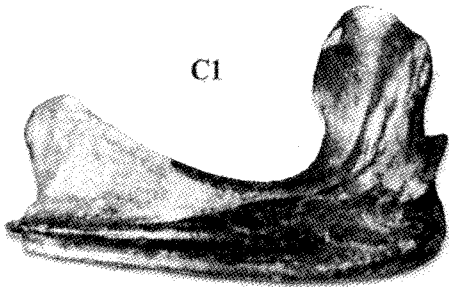
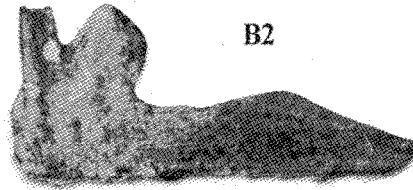
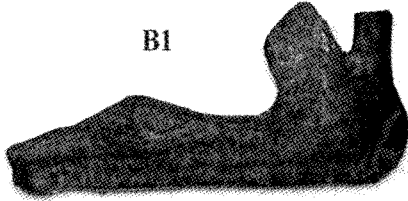
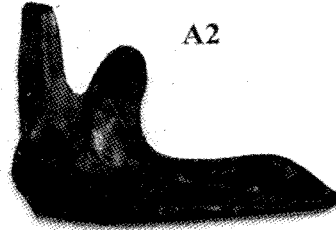
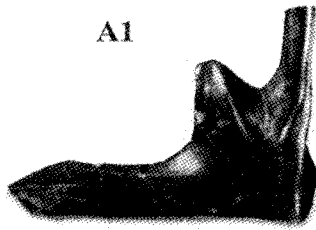
- A. *Acipenser* sp., fragment of skull element (USNM 498660) in external view, Folmer collection.
- B. *Acipenser* sp., fragment of skull element (USNM 498659) in external (B1) and internal (B2) views, Folmer collection.
- C. *Teratichthys antiquitatus*, left dentary (USNM 498656) in internal (C1), dorsal (C2), and external (C3) views, Bennett collection.
- D. *Scomberomorus stormsi*, right dentary (USNM 498861) in internal (D1), external (D2), and dorsal (D3) views, McCloskey collection.
- E. *Brychaetus muelleri*, jaw fragment with four teeth (USNM 498658) in internal (E1), lateral (E2), and external (E3) views, Folmer collection.



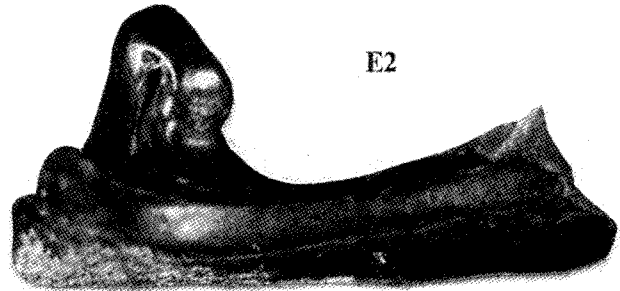
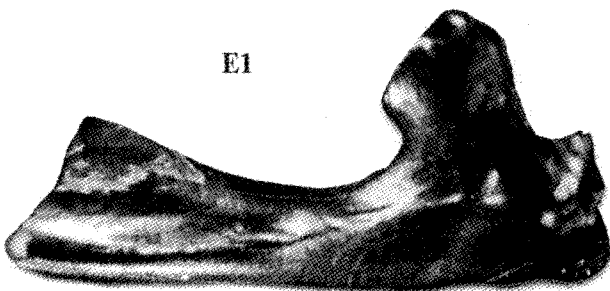


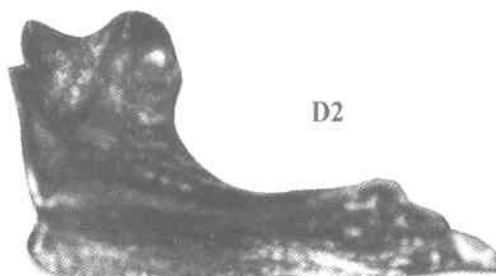
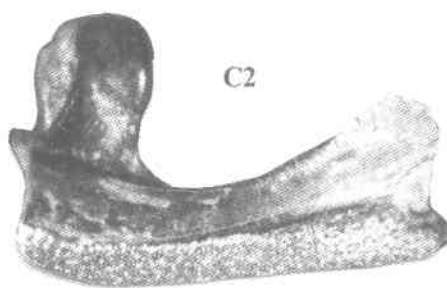
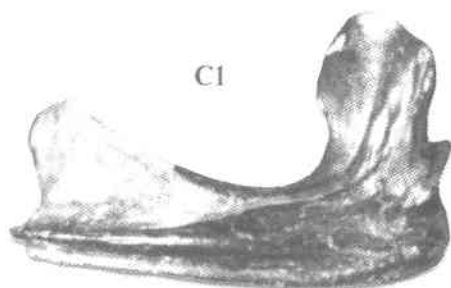
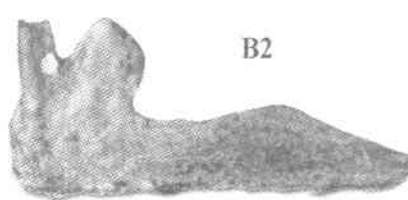
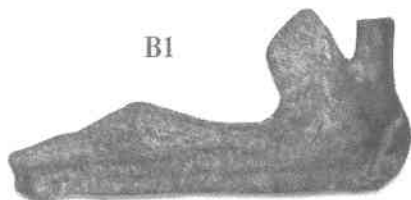
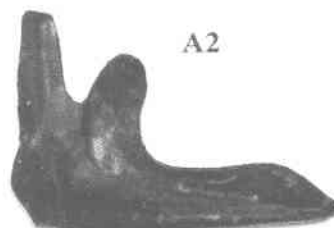
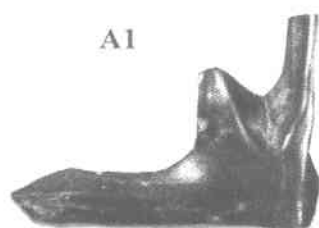
**Plate 4.11.**

- A. Percomorph I, left premaxillary (USNM 498650) in internal (A1) and external (A2) views, Folmer collection.
- B. Percomorph I, right premaxillary (USNM 498651) in external (B1) and internal (B2) views, Folmer collection.
- C. Percomorph D, right premaxillary (USNM 498640) in external (C1) and internal (C2) views, Folmer collection.
- D. Percomorph E, right premaxillary (USNM 498645) in external (D1) and internal (D2) views, Folmer collection.
- E. Percomorph F, right premaxillary (USNM 498648) in external (E1) and internal (E2) views, Folmer collection.

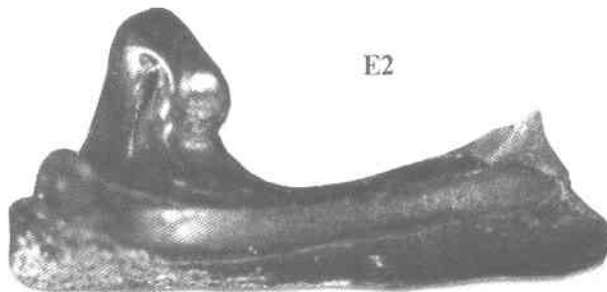
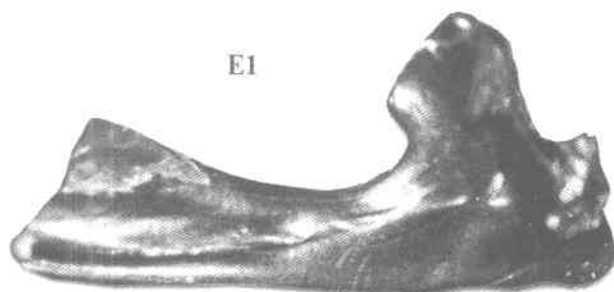


1 cm



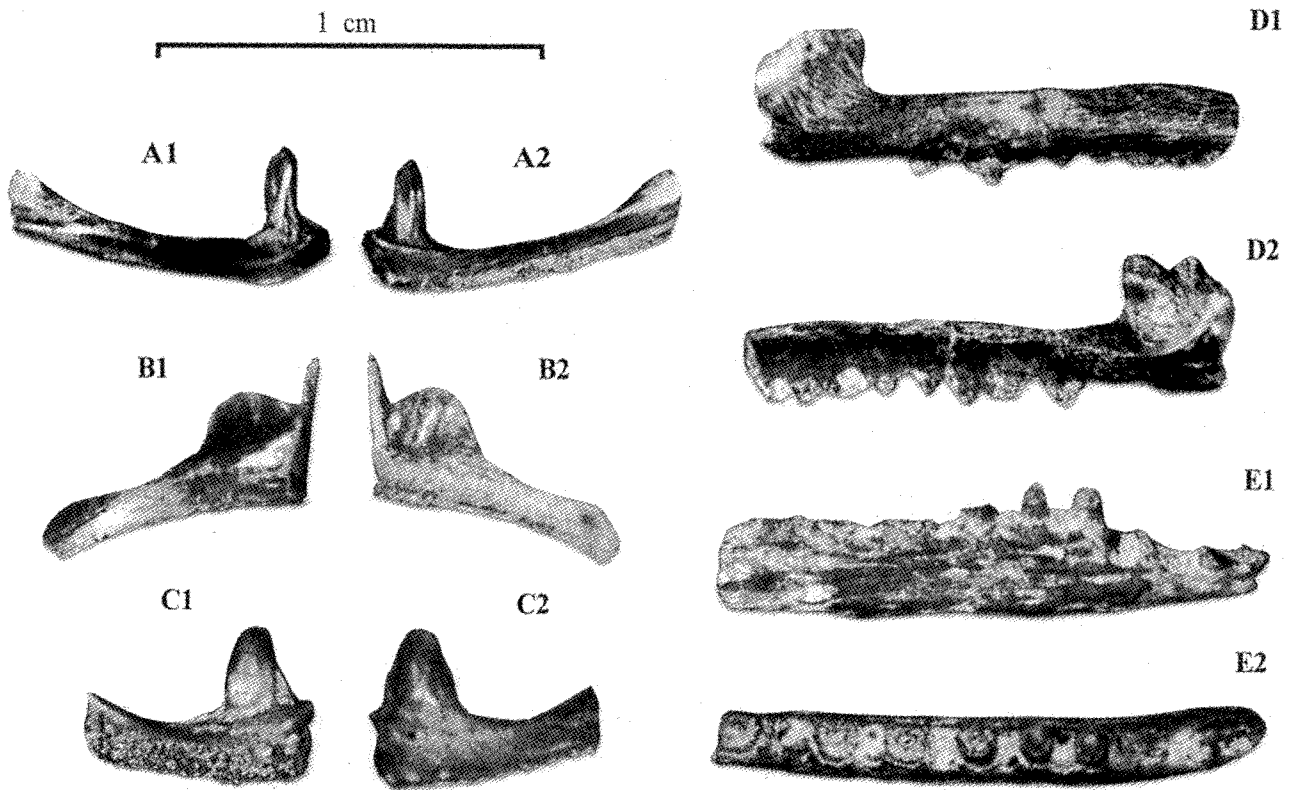


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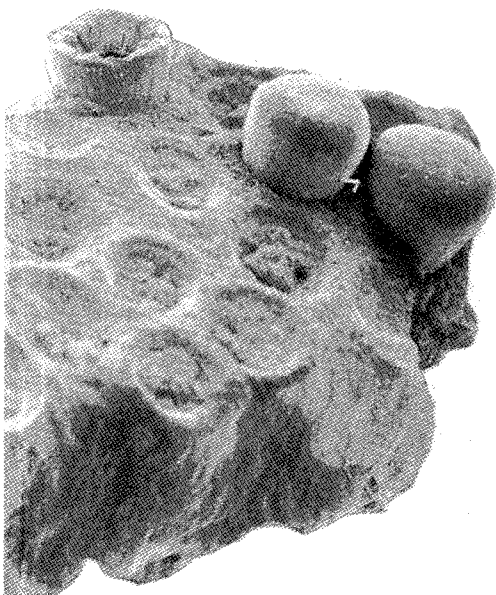
**Plate 4.12.**

- A. Percomorph B, right premaxillary (USNM 498635) in external (A1) and internal (A2) views, Folmer collection.
- B. Percomorph H, right premaxillary (USNM 498657) in external (B1) and internal (B2) views, Folmer collection.
- C. Percomorph G, left premaxillary (USNM 498649) in internal (C1) and external (C2) views, Folmer collection.
- D. *Scombrinus* sp., left premaxillary (USNM 498652) in external (D1) and internal (D2) views, Folmer collection.
- E. *Scombrinus* sp., right(?) dentary fragment (USNM 498653) in external (E1) and dorsal (E2) views, Folmer collection.
- F. *Albula eppsi*, pharyngeal plate (USNM 498661) with teeth in oblique-lateral (F1) view, and two teeth (F2) shown at higher magnification, Folmer collection.



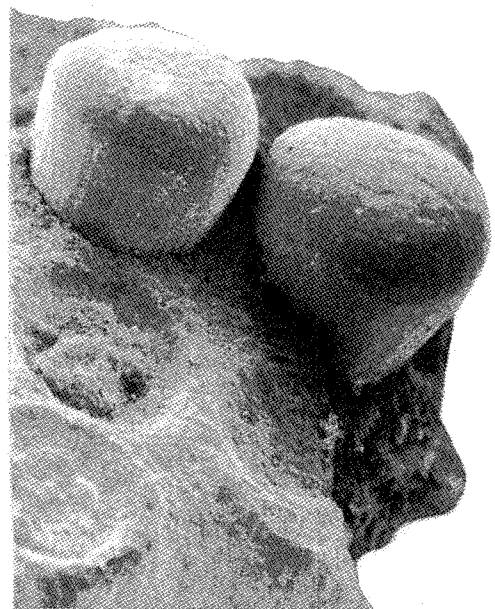
F1

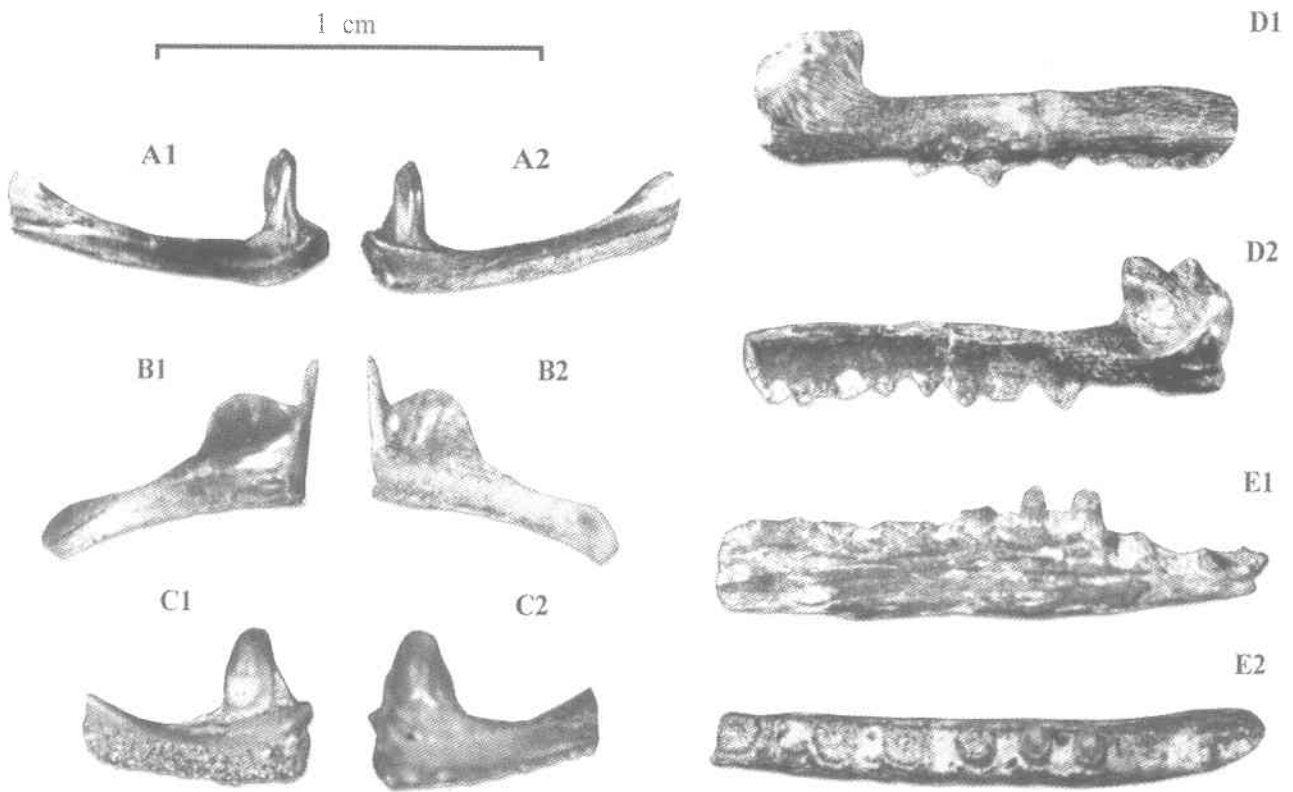
1 mm



F2

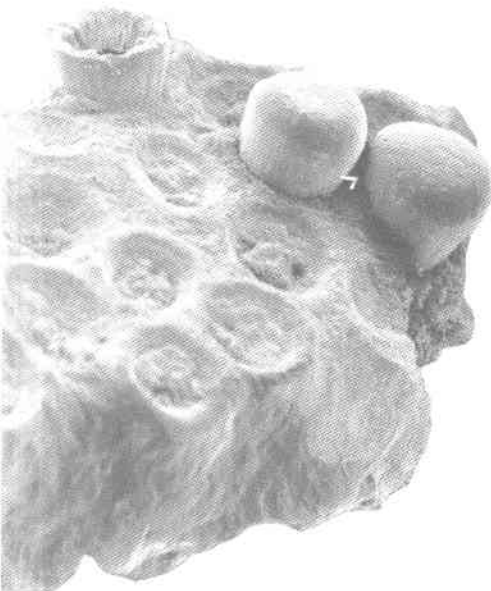
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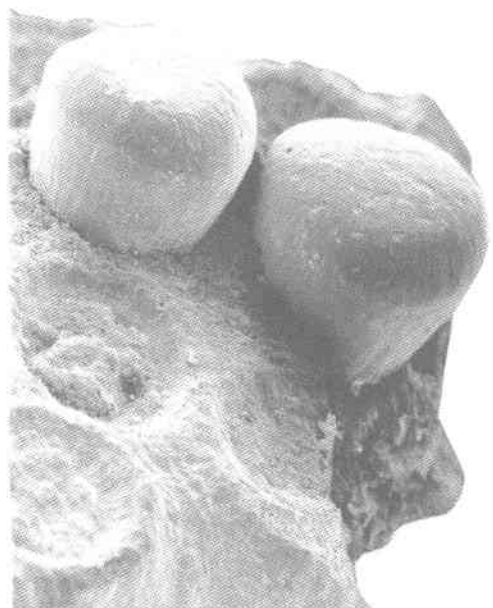
F1

1 mm



F2

1 mm





## PART 5. REPTILE REMAINS FROM THE FISHER/SULLIVAN SITE

Robert E. Weems  
3003 Jonquilla Court, Herndon, VA 20171

### ABSTRACT

Eleven species of early Eocene reptiles have been found in the shallow marine sediments of the Nanjemoy Formation at the Fisher/Sullivan site. These species represent four kinds of turtles, one lizard, three boid snakes, and three crocodylians. Because nine of these taxa also are found in shallow marine strata of the Gulf Coast of the United States and/or western Europe, those nine taxa probably either normally inhabited marine to brackish water environments or were very salt-water tolerant. The occurrence of these taxa over such a wide geographic area indicates that, in early Eocene time, the North Atlantic ocean basin was inhabited by a widespread, cosmopolitan community of shallow marine to coastal reptiles that were able to spread readily around or across the North Atlantic Ocean basin.

### INTRODUCTION

Dinosaurs and their close reptilian relatives were decimated by the terminal Cretaceous extinction event, but diverse turtles, lizards, snakes, and crocodylians survived that catastrophe. Throughout the Paleocene and Eocene, these surviving reptile lineages diversified and either reclaimed or held onto most of the geographic and ecological niches that their Mesozoic ancestors previously had occupied. This renaissance was not to last, however. Starting with the onset of continent-wide glacial conditions in the Antarctic at the beginning of the Oligocene (Barron and others, 1989; Ehrmann, 1998), and the concurrent cooling and drying of the world climate (Frakes, 1979), reptiles underwent a strong decline that has persisted to the present day. In the early Eocene, however, the post-Mesozoic renaissance among the surviving reptilian lineages was at its zenith, for reptiles lived over most of the Earth's surface including the Canadian high Arctic (Hutchison, 1980). This renaissance among Early Tertiary reptiles is reflected in the reptilian fauna from the Fisher/Sullivan site, which includes a suite of reptiles quite different from the ones found in Virginia today.

Most of the reptiles represented among the Fisher/Sullivan fauna were either seagoing or at least tolerant of salt water. This is not surprising, for the Fisher/Sullivan site was on the ocean floor in early Eocene time, many miles east of the Atlantic shoreline. Although land animals and plants have been found at the Fisher/Sullivan site (see parts 6, 7, and 8 of this volume), they are a relatively rare component of the total biota. Therefore, although it is to be hoped that more terrestrial and/or fluvial reptiles will eventually be found from this horizon, only two of the taxa reported here were probably habitually freshwater fluvial or terrestrial in their habitat.

The reptiles that inhabited the early Eocene marine to

marginal marine environment of Virginia show a remarkable diversity, especially when compared to the reptilian fauna of modern coastal waters. Although a comparable diversity of turtles could be cited, large snakes and crocodylians do not inhabit the marine coastal waters of the state today. Thus the coastal ecology of Virginia was very different from what it is today, and this difference in great measure probably reflects a much warmer and /or more equable climate than that which exists in the area today.

**Class Reptilia Laurenti, 1768**  
**Order Chelonia Macartney, 1802**  
**Suborder Cryptodira Cope, 1870**

Of all the reptilian groups represented at the Fisher/Sullivan site, only the turtles have survived to the present time in the coastal Virginia area with something close to their known Eocene level of diversity. One taxon, a softshell turtle belonging to the living family Trionychidae, probably was an inhabitant of both fresh and salt waters. Other forms represented are all sea turtles, belonging to the families Cheloniidae, Toxochelyidae, and Dermochelyidae.

**Family Trionychidae Bell, 1828**  
**Genus Trionyx Geoffroy, 1809**  
*cf. Trionyx pennatus Cope, 1869*

**Figured Specimens:** Fragmentary neural element (USNM 496195) collected by Ron Keil, associated fragments of left sixth? and seventh? costal elements (USNM 496194) collected by Mike Folmer.

**Description:** The neural fragment is flat, without any midline crest or ridge, and its surface is covered with a fine mosaic of pits separated by ridges that are about as wide as the pits. The anterior of the two associated distal costal fragments has a pitted pattern that is more organized than the pattern on the neural, being arrayed in columns that are separated by antero-posteriorly aligned ridges that parallel growth-lines. Within each column, pits are separated by ridges that are more weakly developed than the antero-posterior ridges. Ridges typically are about half as wide as pits. The pattern on the more posterior costal, though reminiscent of the pattern on the costal anterior to it, is less well defined and approaches the kind of pattern seen on the neural. The larger costal fragment is at most 35 mm wide and about 4 mm thick.

**Discussion:** The figured specimens (Plates 5.1, H and 5.2, J) have a pitted to ridged pattern on the surface of the bones

that readily identify them as carapace elements from either a trionychid or carettochelyid turtle. The shape and the pitting pattern of the neural element might occur in either a carettochelyid or a trionychid. The lack of any sutural borders to connect the sixth and seventh costals to peripheral elements, however, is characteristically trionychid because members of the Trionychidae lack peripheral elements (Figure 5-1). The trionychid elements from the Fisher/Sullivan site are all from the same size turtle, and the nature of the preservation is very similar. Therefore, all of this material may well pertain to a single individual.

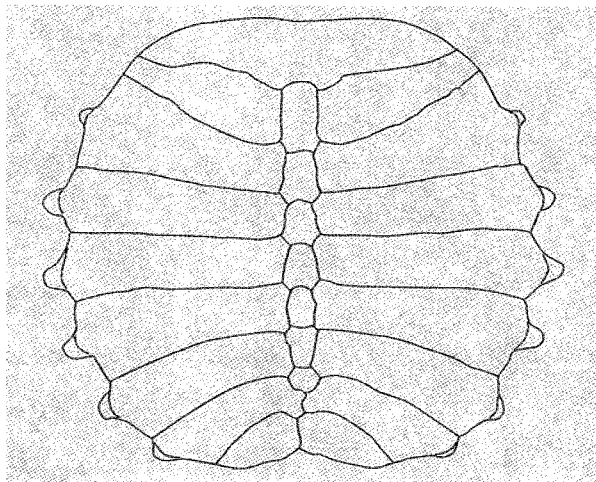


Figure 5.1. The carapace of a trionychid turtle, *Trionyx exquisitus* (after Hay, 1908).

The figured specimens are from a turtle about half the size of the type specimen of *Trionyx pennatus* (Hay, 1908), but otherwise the Fisher/Sullivan site specimens seem comparable to that taxon. Detailed comparison is precluded, unfortunately, because the type specimen of *T. pennatus* is a distal fragment of a more anterior costal element than those among the material available from the Fisher/Sullivan site. However, because the type of *T. pennatus* is the same or nearly the same age as the specimens from the Fisher/Sullivan site, being from the lower Eocene of New Jersey (Cope, 1869; Hay, 1908), and because the two occurrences are only about two hundred miles distant from each other, the material from the Fisher/Sullivan site is tentatively assigned to that taxon until more complete material allows a definitive analysis of its proper taxonomic placement. It should also be noted that there is no certainty that this species, if correctly identified, belongs in the genus *Trionyx*. As what is known of this species is compatible with that genus, however, it is placed there until there is evidence to associate it with another trionychid genus.

Remains of trionychid turtles are found occasionally in marginal marine deposits (for example, Cope, 1869; Weems, 1988), and modern trionychids are occasionally encountered in brackish water (Hay, 1908). For these reasons, it seems probable that at least some trionychids are and were salt-water tolerant. This, in turn, suggests that the presence of this genus at the Fisher/Sullivan site is not unexpected, and that its presence does not indicate the

introduction of a strictly freshwater species into a fauna dominated by marine organisms. Even so, it seems likely that *Trionyx pennatus* also did inhabit fresh and/or coastal waters much of the time.

#### Family Toxochelyidae Baur, 1895

##### Genus Dollochelys Zangerl, 1971

?*Dollochelys* sp.

**Figured specimens:** Fragment of plastron (USNM 496193) collected by Mike Folmer, fragment of mandible (USNM 496192) collected by Ron Keil.

**Description:** Plastral fragment large, thick, and unsculptured. Mandible fragment represents part of the left ramus of a species with a strong and massive jaw; the internal border is crenelated so that the beak probably had a double cutting edge along at least its lateral margins. The anterior portion of the jaw fragment gives no hint that there was an expanded triturating surface.

**Discussion:** The plastron and mandible fragments discussed here (Plate 5.2, C and H) represent a sea turtle of large size. The jaw fragment is not dermochelyid, and all cheloniid sea turtles known from the early Eocene are relatively smaller than this turtle (Moody, 1970). Therefore, these fragments are assigned to the family Toxochelyidae by default. The relatively great length of the mandibular fragment and the absence of any indication of a triturating surface both indicate that this material cannot be assigned to *Erquelinnesia*. Among Early Tertiary toxochelyids, only *Dollochelys* is known to be both large and devoid of a secondary palate and corresponding mandibular triturating surface. This material therefore is assigned questionably to *Dollochelys*, though it easily could pertain to an undescribed taxon.

#### Family Cheloniidae Bonaparte, 1831

##### Genus Puppigerus Cope, 1871

*Puppigerus camperi* (Gray, 1831)

**Figured specimens:** One costal and two neural carapace elements collected by Tom Parks; three peripheral (USNM 496182, USNM 496187; USNM 496191), one costal (USNM 496177), and one neural (USNM 496189) collected by Mike Folmer; fused dentaries collected by Tom Parks, fused dentaries (USNM 496190) collected by Ron Keil; humerus and ulna collected by Tom Parks; proximal end of femur collected by Mike Folmer.

**Supplementary specimens:** Two peripheral elements (USNM 496186, USNM 496183), one neural (USNM 496181), and three costals (USNM 496179, USNM 496180, USNM 496188) collected by Mike Folmer, one costal (USNM 496178) and two neurals (USNM 496184, USNM 496185) collected by Ron Harding.

**Description:** Costal and neural elements are thin and persistently small, and lack any ridges or surface ornamentation. Smaller peripheral elements are not sutured along their proximal border, indicating costoperipheral fontanelles in younger individuals. Larger peripheral elements sometimes show proximal sutures, indicating that the costoperipheral fontanelles tended to disappear with maturity. Dentaries are fused along the midline to form a solid beak, which is elongated and dorso-ventrally flattened.

**Discussion:** The anatomy of *Puppigerus camperi* has been described in considerable detail by Moody (1974), and a typical shell of this taxon is shown in Figure 5.2. Although the morphology of these bones is generalized for a cheloniid, many of the carapace elements from the Fisher/Sullivan site (Plate 5.1, A, B, and G; Plate 5.2, A, D, F, G, and I) can be assigned readily to this taxon. This material represents a turtle that had a shell that was at most only about 40 cm (16 inches) long. The single most diagnostic elements that were recovered are two fused pairs of dentaries (Plate 5.1, C; Plate 5.2, E), which are distinctive because of their long symphysis, narrow anterior angle, and relatively modest size (Figure 5.3). A cheloniid humerus, ulna, and femur head (Plate 5.1, D-F) found at the Fisher/Sullivan site also are of the same size and morphology as those of *P. camperi*. This species appears to have been the most abundant turtle at this site.

*Puppigerus camperi* has been reported from the Eocene of England and Belgium (Moody, 1974), including the London Clay Formation which is correlative with the Potapaco Member of the Nanjemoy. The Fisher/Sullivan site occurrence is the first report of this turtle from the western side of the North Atlantic basin. It also has been found recently

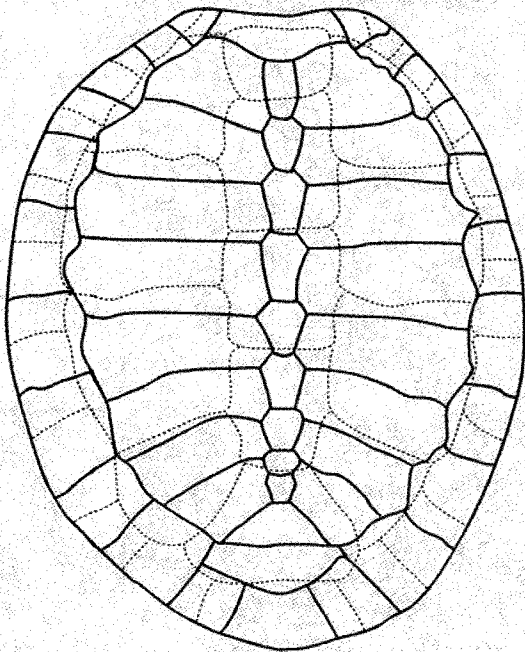


Figure 5.2. The carapace of *Puppigerus camperi* (after Moody, 1974).

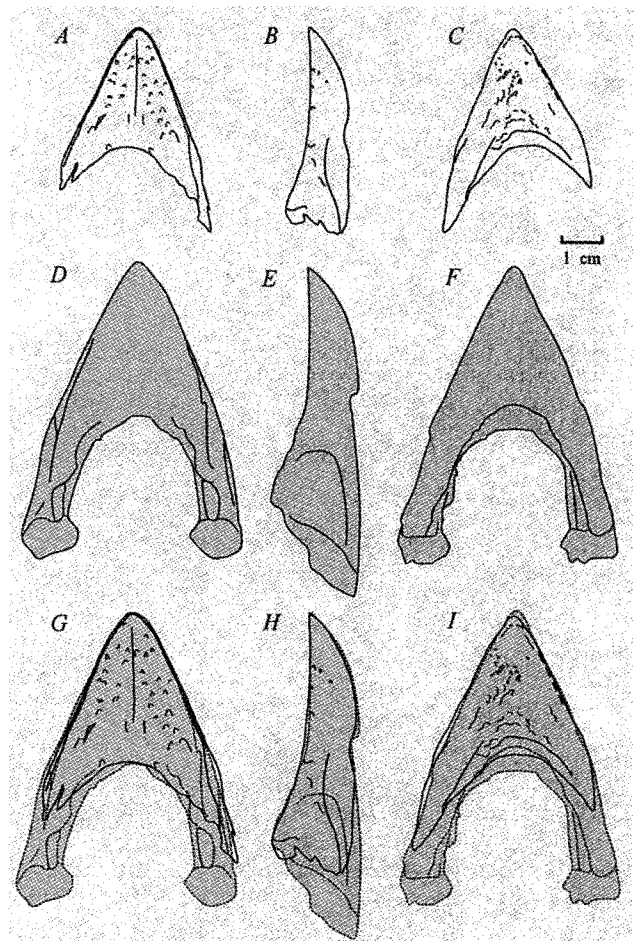


Figure 5.3. The fused dentaries of *Puppigerus camperi* compared with the fused dentaries assigned to that species from the Fisher/Sullivan site. A-C: specimen from the Fisher/Sullivan site in dorsal, lateral, and ventral view. D-F: lower jaw of *Puppigerus camperi* in dorsal, lateral, and ventral view (after Moody, 1974). G-I: top and middle row pictures superimposed on each other.

from the overlying Woodstock Member of the Nanjemoy Formation near Popes Creek, Maryland. Weems (1988) suggested that *Catapleura ruhoffi* from the upper Paleocene Aquia Formation was ancestral to *Puppigerus camperi*, and the occurrence of the latter form throughout the overlying Nanjemoy Formation strengthens this suggestion.

**Family Dermochelyidae Baur, 1888**

**Genus Eosphargis Lydekker, 1889**

cf. *Eosphargis gigas* (Owen, 1861)

**Figured specimen:** Left frontal bone (USNM 496196) collected by Mike Folmer.

**Description:** Left frontal bone from the skull of a large sea turtle, bordered on all sides by sutural boundaries.

**Discussion:** A left frontal bone (Plate 5.2, B), pertaining to a large turtle, is completely bordered by sutural contacts. There is no hint of any beveled external border, such as would be present if this bone formed a part of the orbital rim for the eye. The only group of Cenozoic sea turtles that does not provide a contribution from the frontals to the orbital rim is the Dermochelyidae, so this bone can be readily assigned to that family (Figure 5.4). A generic and specific placement is more problematic, however, because the sutures on the type skull of *Eosphargis gigas* have not been delineated. Because the frontal element from the Fisher/Sullivan site could be comparable to the frontal of *Eosphargis gigas*, which was described from the London Clay and is the same age as the specimen from the Fisher/Sullivan site, and because no other dermochelyids are known from the early Eocene, this material is tentatively assigned to that taxon. At present, however, rigorous comparison is impossible, and it remains possible that this specimen could pertain to an unnamed taxon.

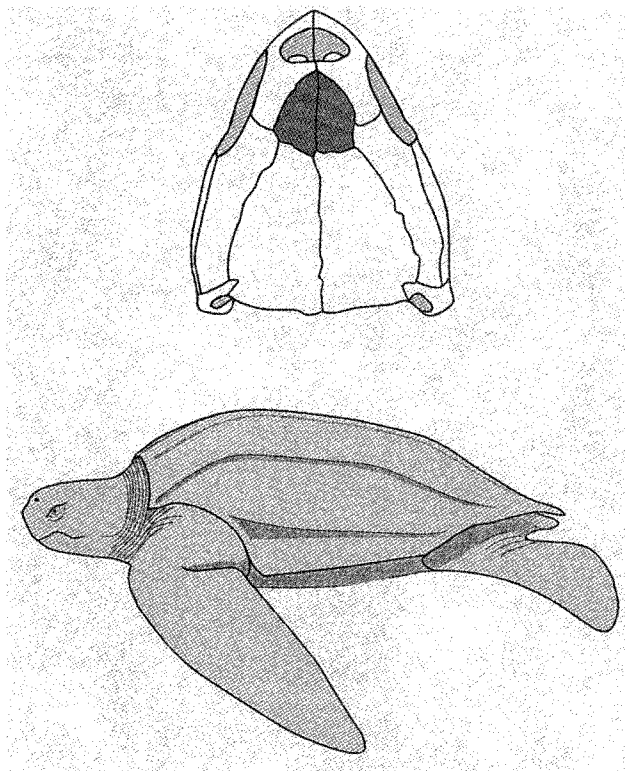


Figure 5.4. Appearance of the living dermochelyid turtle, *Dermochelys coriacea* (after Müller, 1968). Inset at top shows the bones of the skull in dorsal view. Frontals are shown in dark gray.

**Order Squamata Oppel, 1811**  
**Suborder Lacertilia Owen, 1842**

Lizards typically are terrestrial in habitat, though a few are semi-aquatic (Estes, 1964). For this reason, it is remarkable that even a single fragmentary left dentary from

this group was recovered at the Fisher-Sullivan site. Almost certainly, this specimen represents an instance of a terrestrial animal that was washed into a shallow marine depositional setting far from the animal's normal habitat.

**Infraorder Anguimorpha Furbinger, 1900**

**Family Anguidae Gray, 1825**

**Genus Parophisaurus Sullivan, 1987**

*Parophisaurus mccloskeyi* sp. nov.

**Figured specimen:** Left dentary (USNM 498662), containing two teeth and missing anterior and posterior ends, collected by Mike McCloskey.

**Diagnosis:** Dentary elongate and shallow, with its external border bearing widely-spaced dimpled foraminae located mostly near the ventral border of the jaw ramus, and its dorsal surface bearing a pleurodont dentition. Teeth smooth, linguo-labially compressed, antero-posteriorly elongate, and separated by gaps about one-fourth as wide as the teeth. Tooth crowns high, linguo-labially compressed to form a cutting edge, pointed, strongly curved along their anterior borders, and nearly straight along their posterior borders. Cutting edges aligned in parallel along the axis of the outer edge of the jaw ramus. Tooth bases show no hint of basal excavations, indicating an alternate tooth-replacement pattern.

**Description:** Nearly complete dentary, missing a small portion of its anterior and posterior ends, elongate, nearly straight, and containing a single row of pleurodont teeth. Tooth row includes two adjacent complete teeth, bases of five teeth, and three empty sockets. Teeth hollow, fused to dentary, and separated by gaps about one-fourth as wide as the teeth. Base of teeth subrounded, flattened along their labial border, and tapered upward. Tooth crowns pointed, smooth, strongly curved along their anterior border, nearly straight along their posterior border, and slightly worn at their tips. Base of teeth bear no indication of basal excavations caused by replacement teeth.

**Discussion:** The antero-posteriorly elongate shape of the teeth and the pleurodont dentition pattern readily characterize this dentary as lacertilian (Plate 5.4, B-C). Among lizards, only members of the infraorder Anguimorpha (excluding the family Xenosauridae) and a few members of the family Teiidae lack basal excavations along the internal base of their teeth, formed by the presence of growing replacement teeth (McDowell and Bogert, 1954; Estes, 1964, p. 127). As teiids have complexly shaped tooth crowns (Estes, 1983), totally unlike the teeth in this jaw, the specimen described here pertains to an anguimorph.

Infraorder Anguimorpha contains two superfamilies, the Anguinoidea and the Platynota. Platynota, which includes varanids, necrosaurids, and helodermatids, have strongly

recurved, conical, and pointed teeth with basal striations that look nothing like the teeth described here. Therefore, this specimen belongs among the Anguinoidea. The Anguinoidea includes three families, Xenosauridae, Dorsetosauridae, and Anguidae. Because the Dorsetosauridae are remote in time (Jurassic) and the Xenosauridae have basal excavations on the internal edge of their teeth, this specimen belongs among the Anguidae.

The Anguidae are divided into five subfamilies: Anguinae, Anniellinae, Glyptosaurinae, Gerrhonotinae, and Diploglossinae. Among the numerous genera included in these various families and subfamilies, only *Apodosauriscus* in the Anniellinae, and *Exostinus*, *Machaerosaurus*, *Ophisaurus*, and *Parophisaurus* in the Anguinae have teeth at all similar to the ones seen here (Estes, 1983). Although *Apodosauriscus* bears similar teeth, those teeth are closely appressed antero-posteriorly and are relatively more elongate than the teeth described here. The teeth of *Ophisaurus acuminatus* also are similar in shape, but the ramus of the dentary beneath them is much deeper than in the jaw described here. Moreover, the age (late Miocene) and provenance (Europe) of *O. acuminatus* are remote, while western hemisphere species assigned to *Ophisaurus* do not have teeth at all similar to the teeth in the jaw described here. All of these factors weigh strongly against assigning this specimen to *Ophisaurus*. Two species of anguins (*Parophisaurus pawneensis*, from the Oligocene of Colorado, Wyoming, and Nebraska, and *Machaerosaurus torrejonensis*, from the Paleocene of New Mexico) show strong similarity to the specimen at hand. Neither taxon is very remote in time from the Fisher/Sullivan site species, and either taxon easily could have ranged into the eastern United States.

While assignment to either genus would be reasonable, the tooth morphology of this specimen is closer to that of *Parophisaurus pawneensis* than *Machaerosaurus torrejonensis*. The dentary teeth of *M. torrejonensis* bear a distinct groove on their labial surface that is not present on the teeth of the specimen described here, and they are consistently narrower (Sullivan, 1982). The teeth of *P. pawneensis* are more similar in their width, height, and uniformly smooth surfaces. *P. pawneensis*, however, has a jaw ramus that is significantly deeper than that of the Fisher/Sullivan site specimen (Sullivan, 1987), and this characteristic debars placement of this specimen in the described species. For this reason, this specimen is designated as a new species, *Parophisaurus mccluskeyi*. It is entirely possible that *M. torrejonensis*, *P. mccluskeyi*, and *P. pawneensis* represent a single lineage within the Anguinae.

*Parophisaurus pawneensis* had limbs that were functional but diminutive relative to the limbs of most lizards (Sullivan, 1987). Modern anguines have taken this trend to the extreme of becoming entirely limbless and snake-like in appearance (Bauer, 1992). Although there is no direct evidence available concerning the nature of the limbs of *P. mccluskeyi*, it can be reasonably inferred that it had diminutive limbs and moved in a rather snake-like manner.

## Suborder Serpentes Linnaeus, 1758

Three kinds of snakes, all boids referable to the extinct family Palaeophidae, are represented among the material from the Fisher/Sullivan site. Palaeophids have been found consistently in marine to marginal marine depositional environments, and there is little doubt that they were primarily coastal to oceanic marine animals. *Palaeophis* has been found in Africa in rocks as old as Late Cretaceous (Rage and Wouters, 1979), but the genus is known in North America only in sediments as old as the late Paleocene (Lynn, 1934). Therefore, it seems likely that the genus originated in Africa during the Cretaceous, and did not spread to North America until the Paleocene. The family apparently did not survive past the Eocene, but ecologically its role may be occupied today by the cobrid sea snakes of the tropical Indo-Pacific region. No snakes today habitually inhabit the marine waters of the Atlantic Ocean basin.

A related but smaller fossil snake in the family Palaeophidae, *Archaeophis proavus* from the early Eocene beds of Monte Bolca in Italy, is known from a whole body impression. According to Janensch (1906), the specimen of *Archaeophis* from Monte Bolca has a total of 565 vertebrae in its body, 454 of which represent the neck and trunk and 111 of which represent the tail. *Palaeophis* probably had a similarly large number of vertebrae. For now, *Archaeophis* (Figure 5.5), is the best model available for envisioning the appearance of *Palaeophis*.

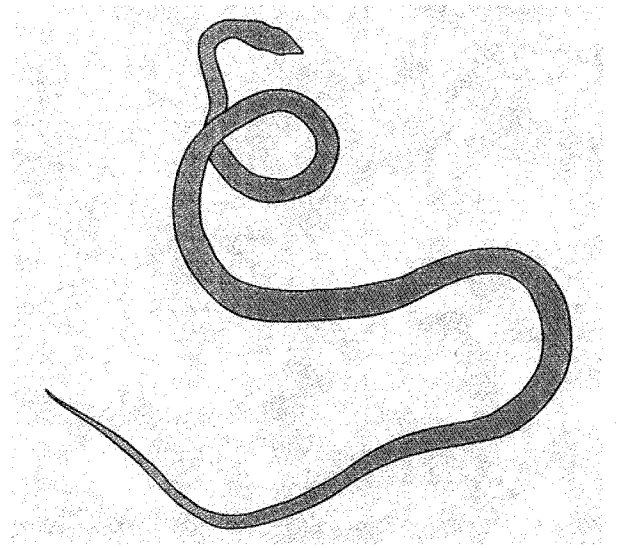


Figure 5.5. Body form of *Archaeophis proavus*, the only representative of the family Palaeophidae for which the body proportions are known (after Janensch, 1906).

## Family Palaeophidae Boulenger, 1882

### Genus Palaeophis Owen, 1840

*Palaeophis toliapicus* Owen, 1841

**Figured specimens:** Two vertebrae (USNM 496200, USNM 496202) and a tooth (USNM 496205) collected by Mike Folmer.

**Supplementary specimens:** Two vertebrae (USNM 496199, USNM 496203) collected by Mike Folmer, three vertebrae (USNM 496201, USNM 496204, USNM 496206) collected by Chuck Ball.

**Description:** Procoelous vertebrae with typical serpentine zygosphenes-zygantrum articulations in addition to the normal prezygapophysis-postzygapophysis articulations between vertebrae, vertebral centra moderately elongate with length about twice their height, neural spine typically occupying one-half or more of the length of the neural arch. Teeth long, slender, and recurved, with a deep and long root canal at their base.

**Discussion:** Nearly two hundred vertebrae referable to *Palaeophis* have been recovered from the Fisher/Sullivan site, and all but three appear to be referable to *P. toliapicus*. Many are isolated specimens, but at least three articulated trunk vertebrae were collected from the site by Barbara Ermler. Two exceptionally well preserved vertebrae are illustrated in Plate 5.3, C and D. *Palaeophis toliapicus* was originally described from shallow marine beds of the early Eocene London Clay (Owen, 1841), and it is not surprising to find this taxon represented in shallow marine beds of the same age in Virginia. Another nominal taxon, *Palaeophis littoralis* from the early Eocene Manasquan Marl of New Jersey (Cope, 1868) and Mississippi (Parmley and Case, 1988), is very similar to the specimens from the Fisher/Sullivan site. Rage (1984) has suggested that *P. toliapicus* and *P. littoralis* may be synonymous. The material available from the Fisher/Sullivan site seems to include specimens that grade continuously between the morphology of the two nominal species, and this supports the contention that only a single species is represented by all of this material. Therefore, all of the material cited above from Mississippi, Virginia, New Jersey, and England is included here under the name *Palaeophis toliapicus*.

Three teeth are tentatively associated with this species based on their size and snake-like appearance, one of which is shown in Plate 5.3, A. These are long and sharp, which suggests that they came from a fish or squid-eating animal. Because of their great length and delicate form, they probably were not particularly strong. This suggests that *P. toliapicus* was capable of piercing and grasping its prey while it swallowed, but it did not use its teeth to hold large active prey that was still struggling. This could imply that the prey of *Palaeophis toliapicus* were not particularly large or powerful creatures, relative to its size. Modern boids, which are the closest living relatives to the palaeophids, often crush their prey with their bodies before they swallow it, so the relatively delicate dentition does not necessarily mean that these snakes were incapable of killing a large animal if they were able to successfully grip it with their bodies.

Despite the fact that bones of *Palaeophis* have been recognized in the fossil record for 150 years, the appearance

and habitat of the various species within this genus remain enigmatic because only vertebrae, ribs, and possibly teeth have been found to date. At the Fisher/Sullivan site, vertebrae referable to *Palaeophis toliapicus* range from 3 to 18 mm in centrum length, which indicates that individuals from juvenile to adult size are represented. Such a wide age range suggests that palaeophids spent their entire lives in the ocean, which in turn suggests that they probably were live-bearers that did not return to the land to lay eggs. This hypothesis is plausible because, although pythons lay eggs, most boas retain their eggs within their body and thereby bear live young (Shine, 1992). Another possible adaptation for marine life is suggested by the fact that the vertebrae of *Palaeophis* are somewhat compressed from side to side, relative to the vertebrae of boas. This suggests that these snakes had bodies that were somewhat flattened side to side, as in marine eels and living sea snakes (which are members of the cobra family and not descendants of the palaeophids).

The Fisher/Sullivan fauna contains the first reported occurrences of this species from the Maryland-Virginia region, though two specimens mentioned in Weems (1984) ("*Palaeophis virginianus*" from the Potapaco Member and the unnamed small palaeophid from the Woodstock Member of the Nanjemoy Formation) on re-examination appear to be referable to this taxon as well. Therefore, *Palaeophis toliapicus* ranges throughout the Nanjemoy Formation.

Based on the allometric proportions suggested by Holman (1982), the vertebrae of *Palaeophis toliapicus* from the Fisher/Sullivan site may represent individuals that ranged from about 1.5 to 13 feet in length, the latter size presumably being about the maximum size of this species. Owen (1841) estimated that the type material of *P. toliapicus* represented a snake about 10 feet in length.

*Palaeophis casei* Holman, 1982

**Figured Specimen:** One vertebra (USNM 496197) collected by Mike Folmer.

**Supplementary specimen:** One vertebra (USNM 496198) collected by Chuck Ball.

**Description:** Very small procoelous vertebrae with typical serpentine zygosphenes-zygantrum articulations in addition to the normal prezygapophysis-postzygapophysis articulations between vertebrae. Vertebral centrum elongate, with length about three times greater than the height. Neural spine typically occupies only the posterior third of the neural arch.

**Discussion:** Most of the snake vertebrae from the Fisher/Sullivan site are referable to *Palaeophis toliapicus*, but two small vertebrae (Plate 5.3, B) are much longer proportionally than the others, having a centrum length:height ratio of 3:1 instead of 2:1 as is typical of *P. toliapicus*. These unusual specimens also have an exceptionally low neural spine that is restricted to the posterior third of the neural arch. These

characteristics, as well as the small size (4 mm maximum length) are typical of the small palaeophid snake, *Palaeophis casei*. Previously, this taxon has been reported only from estuarine strata of the Bashi Marl and the Tusahoma Formation of Mississippi (Holman, 1982; Parmley and Case, 1988). As the age of the beds in Mississippi are close to or identical with the age of the beds at the Fisher/Sullivan site, it is not particularly surprising that this species also has shown up in Virginia. The extremely small size of this species, however, makes it very unlikely that its vertebrae will be found without the use of screening and picking. Holman (1982) estimated that the adult of this species was probably only about 50 cm (20 inches) in length. Because of its size and the depositional setting in which the type material was found, he also concluded that it normally inhabited estuarine environments and ate small fish.

*Palaeophis virginianus* Lynn, 1934

**Figured Specimen:** One vertebra (USNM 494368) collected by Ron Keil.

**Description:** Very large procoelous vertebra with typical serpentine zygosphenes-zygantrum articulations in addition to the normal prezygapophysis-postzygapophysis articulations between vertebrae. Vertebral centrum moderately elongate, with length about twice the height. Neural spine typically occupies two-thirds or more of the neural arch. Prezygapophysial processes elongated and robustly developed.

**Discussion:** One *Palaeophis* vertebra from the Fisher/Sullivan site is notably larger than all of the rest (Figure 5.6, Plate 5.4A). On the basis of both its size and its widely flared and robust prezygapophysial processes, the specimen readily can be assigned to the species *Palaeophis virginianus* Lynn. The only other palaeophid known from the Chesapeake Bay region that approaches the size of this specimen is *Palaeophis grandis* (Blake, 1941), but in that taxon the prezygapophysial processes are not so greatly expanded outward, as is seen in this specimen. *Palaeophis virginianus* is by far the largest snake found at the Fisher/Sullivan site. It probably attained a length of about 18 feet (Holman, 1982).

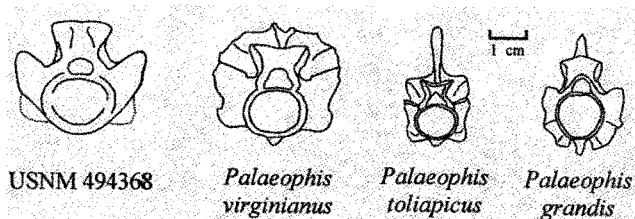


Figure 5.6 Anterior view of *Palaeophis virginianus* vertebra (USN 494368) from the Fisher/Sullivan site compared with anterior views of vertebrae of *Palaeophis virginianus*, *Palaeophis grandis*, and *Palaeophis toliapicus*. Note that only *P. virginianus* has elongate and robust prezygapophysial processes.

This is the first specimen of this species reliably reported from the Potapaco Member of the Nanjemoy Formation, so it represents a significant temporal extension for this species upward from the underlying Paspotansa Member of the Aquia Formation (Lynn, 1934). *P. virginianus* has been reported from the Tallahatta Formation of Alabama (Holman and Case, 1988), but the specimen figured is more probably *P. grandis* based on its relatively narrow prezygapophysial processes, its very antero-posteriorly elongated neural spine, and its stratigraphic horizon.

**Order Crocodilia Gmelin, 1788**  
**Suborder Eusuchia Huxley, 1875**

At least three kinds of crocodilians inhabited the coastal waters of Virginia during the early Eocene. All of these forms also occur in western Europe, and this suggests that all three taxa were either marine in habit or at least tolerant of salt water. This is unusual, compared to the habitat preferences of most modern crocodilians, though the salt-water crocodile (*Crocodylus porosus*) is caught alive and well in marine waters around Indonesia today. The diversity of Eocene crocodilians is remarkable when one considers the total absence of these creatures in Virginia at the present time.

**Family Gavialidae Adams, 1854**  
**Genus Eosuchus Dollo, 1907**  
*Eosuchus lerichei* Dollo, 1907

**Figured Specimens:** Premaxillaries (USNM 498862) collected by Ron Ison, dermal scute (USNM 496211) collected by Jim Savia, two isolated teeth collected by Tom Parks.

**Supplementary Specimens:** Anterior (USNM 496212), lateral (USNM 496214), and posterior tooth (USNM 496215) collected by Mike Folmer, posterior tooth (USNM 496213) collected by Ron Harding, rhomboidal and rounded dermal armor (USNM 496209, USNM 496210) collected by Mike Folmer.

**Description:** Premaxillaries in dorsal view surround narial opening, in ventral view contain sockets for five pairs of teeth. First and fourth tooth sockets distinctly larger than the second, third, and fifth. Nasals located far behind narial rim. Teeth small, recurved and strongly fluted. Anterior teeth generally conical and elongate, posterior teeth stouter and laterally compressed. Dermal scutes small and typically lack a dorsal keel, though faint ridges may occur on scutes from the mid-region of the back.

**Discussion:** The type material of *Eosuchus lerichei*, a small crocodilian from the early Eocene of northern France, was described by Dollo (1907). The skull, figured later by Swinton (1937), has a narrow and elongated rostrum (Figure 5.7). A pair of premaxillaries from the Fisher/Sullivan site (Plate 5.5, A-E) are nearly identical in size and appearance to the

premaxillaries of the type skull and can be assigned to *E. lerichei* with some confidence. Persistently small, fluted and recurved crocodilian teeth (Plate 5.3, G and H), similar in size and diameter to the alveolae of the premaxillaries of *E. lerichei*, are somewhat more tentatively assigned to this taxon. Similarly, small to moderate-sized crocodilian dermal scutes (Plate 5.3, I), lacking a dorsal keel or bearing only a poorly developed keel, also are assigned to this taxon.

*Kentisuchus spenceri* from the lower Eocene London Clay of England (Owen, 1850) and *Dollosuchus dixonii* (Owen, 1850; Swinton, 1937) from the middle Eocene of Belgium and England are closely related to *Eosuchus*. They differ significantly, however, in that their nasal elements are more elongated and extend forward to touch the posterior rim of the narial opening. A small crocodilian species from New Jersey, described as *Thecachampsoides minor* (Norell and Storrs, 1989) and based on the fragmentary basicranial region of a skull and a few associated vertebrae, comes from a unit that is identical in age to the Potapaco Member of the Nanjemoy Formation. *T. minor* does not differ in any obvious way from the specimens of *Eosuchus lerichei* so far recovered from the Nanjemoy Formation, but direct comparison is impossible because no common skeletal elements are yet known.

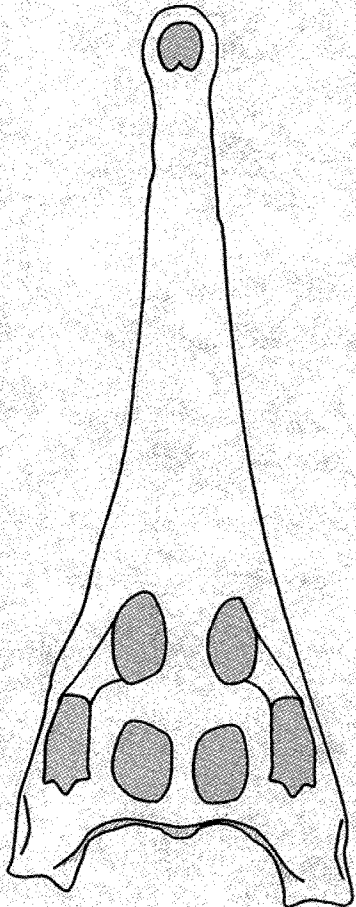


Figure 5.7. The skull proportions of *Eosuchus lerichei* in dorsal view (after Swinton, 1937).

The elongated, gavial-like snout of *Eosuchus* strongly suggests that this crocodilian was piscivorous. The fact that *E. lerichei* is the most common crocodilian in the shallow marine beds of the Fisher/Sullivan site, as well as the fact that it ranged across the Atlantic basin to France, suggests that this species probably frequented shallow marine environments. Locally, it is known from both the late Paleocene Aquia and the early Eocene Nanjemoy Formations.

*Eosuchus* and *Thoracosaurus* (discussed next) are both thoracosaurine crocodilians. Recently, Poe (1996) removed thoracosaurines from the family Crocodylidae and placed them in the family Gavialidae. This taxonomic placement is followed here, though the change remains controversial (Brochu, 1997).

#### Genus *Thoracosaurus* Leidy, 1852

*Thoracosaurus neocesariensis* (de Kay, 1842)

**Figured specimen:** One tooth (USNM 496208) collected by Mark Bennett.

**Description:** Tooth large, moderately elongate, round in its basal section, and possessing enamel striations but not fluting.

**Discussion:** An isolated large tooth (Plate 5.3, F) appears to be referable to this long ranging species of crocodilian. *Thoracosaurus neocesariensis* ranges from Late Cretaceous through early Eocene strata of New Jersey (Miller, 1955; Steel, 1973; Carpenter, 1983), and a closely related species is known from the early Paleocene of Denmark (Troedsson, 1924). The occurrence of this species at the Fisher/Sullivan site is among the youngest known in the eastern United States. Even though *Thoracosaurus neocesariensis* (Figure 5.8) looked superficially somewhat like *Eosuchus lerichei*, it was a much larger crocodilian with a more elongated snout that bore teeth that were widely separated from one another. Additionally, although the teeth of this species had enamel that was somewhat crinkled on a fine scale, they are not truly fluted as are the teeth assigned here to *Eosuchus lerichei*.

Because the skull and teeth of *Thoracosaurus* are grossly similar to those of *Eosuchus*, both species probably were specialized for catching fish. The teeth in *Thoracosaurus*, however, are more robust and attain much larger sizes. This suggests that *Thoracosaurus* probably was capable of attacking much larger prey than *Eosuchus*, such as large fish or other reptiles such as turtles.

#### Family Alligatoridae Gray, 1844

##### Genus *Diplocynodon* Pomel, 1847

*Diplocynodon hantoniensis* (Wood, 1844)

**Figured specimen:** One tooth (USNM 496207) collected by Ron Harding, dermal scute collected by Ron Keil.

**Description:** Tooth large and laterally compressed, apex blunt and somewhat rounded. Dermal scute large, bearing a prominent dorsal ridge.

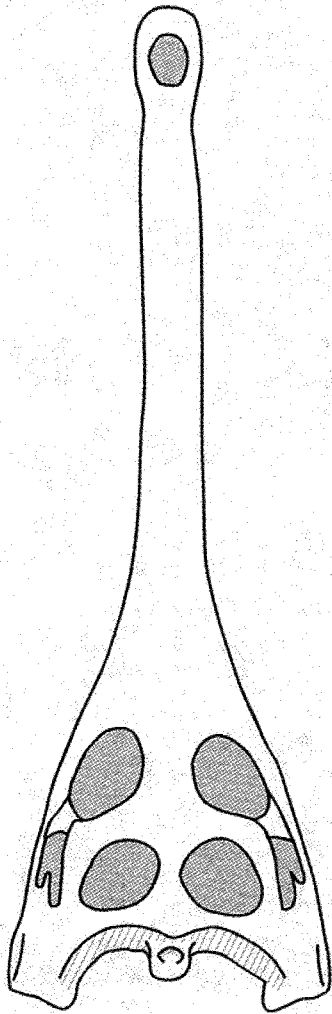


Figure 5.8. The skull proportions of *Thoracosaurus neocesariensis* in dorsal view (after Carpenter, 1983).

large and robust to belong to *Eosuchus*.

The tooth of *Diplocynodon* is larger than any other crocodilian tooth found so far at the Fisher/Sullivan site. The blunt, crushing design of the tooth, and of the entire dentition in complete skulls of this species, indicates that the animal typically crushed rather than pierced its prey. This specialization is especially helpful for crushing turtles, which may have been its normal prey. Although this genus is so far unknown from anywhere else in the Pamunkey Group, its long range in the British Early Tertiary section suggests that it also might be expected to occur in the underlying Aquia Formation or the overlying Piney Point Formation. Its rarity in the Pamunkey Group, and its abundance in Britain only in beds that are fluvial to marginal marine, suggests that it was not an animal that normally inhabited marine environments.

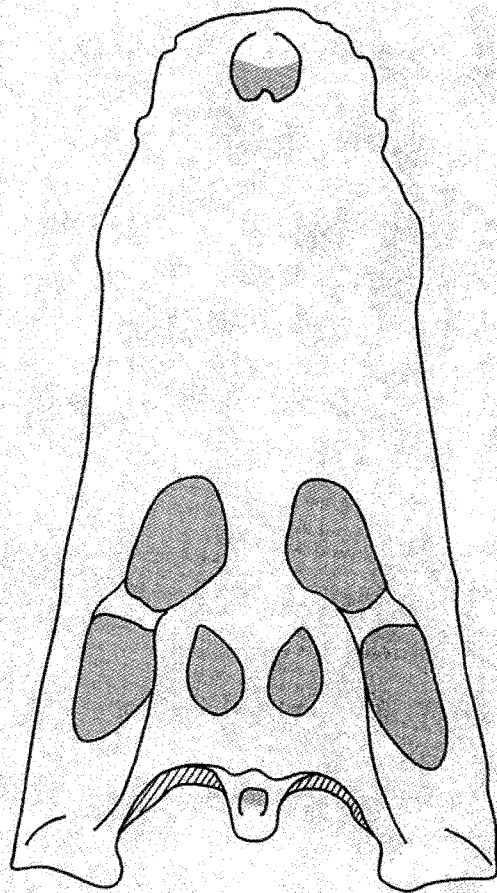


Figure 5.9. The skull proportions of *Diplocynodon hantoniensis* in dorsal view (after Benton and Spencer, 1995).

**Discussion:** An isolated large tooth of a crocodilian (Plate 5.3, E) clearly pertains to a taxon different from those described previously. It is very large and very blunt in its overall appearance, having a crushing alligator-like morphology rather than a piercing crocodile-like morphology. This tooth is indistinguishable from ones assigned to the blunt-snouted alligatorine *Diplocynodon hantoniensis* (Figure 5.9). Although the type material of *Diplocynodon* is from the late Eocene Lower Headon beds of England (Benton and Spencer, 1995, p. 284), the species has been reported from as far down in the British column as the upper Paleocene (Benton and Spencer, 1995, p. 276), and a related species of *Diplocynodon*, *D. stuckeri*, has been reported from the middle Eocene of Wyoming (Mook, 1960). Therefore, it is reasonable to assign the eastern American alligatorine tooth from the Fisher/Sullivan site to this species. A large piece of unkeeled crocodilian armor (Plate 5.2, K) is tentatively assigned to this taxon as well, because alligatorine armor scutes have strong dorsal keels (Olsen, 1968). In contrast, the dermal armor of *Thoracosaurus* was not keeled (Carpenter, 1983), and the specimen seems too

## DISCUSSION

Of the 11 taxa that make up the reptilian fauna from the Fisher/Sullivan site, five were probably fully marine (?*Dollochelys* sp., *Puppigerus camperi*, cf. *Eosphargis gigas*, *Palaeophis toliapicus*, *Palaeophis virginianus*), two were either fully marine or marginally marine (*Eosuchus lerichei*, *Palaeophis casei*), and two were probably at least

salt-water tolerant (*Thoracosaurus neocesariensis*, cf. *Trionyx pennatus*) (Table 1). Only the crocodilian *Diplocynodon hantoniensis* and the lizard *Parophisaurus mcclloskeyi* probably did not normally inhabit marine environments. The diversity of this salt-water-tolerant assemblage indicates that the marine to marginal marine environment of the southeastern United States in the early Eocene supported a much more varied suite of reptiles than it does today. This obvious contrast with the modern fauna probably will become even more pronounced in the future, for there are numerous other marine reptilian taxa, so far unknown from the Fisher/Sullivan site, that occur elsewhere in the Pamunkey Group of Maryland (Weems, 1988) and the London Clay of England (Benton and Spencer, 1995). Most likely of these to be found are a number of chelonoid sea turtles, such as *Argillochelys*, *Eochelone*, *Erquelinnesia*, and *Neurochelys*.

**Table 1. Taxonomic summary of the reptiles found at the Fisher/Sullivan site**

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Order Chelonia	
Family Trionychidae	
	cf. <i>Trionyx pennatus</i>
Family Toxochelyidae	
	? <i>Dollochelys</i> sp.
Family Cheloniidae	
	<i>Puppigerus camperi</i>
Family Dermochelyidae	
	cf. <i>Eosphargis gigas</i>
Order Squamata	
Suborder Lacertilia	
Family Anguidae	
	<i>Parophisaurus mcclloskeyi</i>
Suborder Serpentes	
Family Palaeophidae	
	<i>Palaeophis casei</i>
	<i>Palaeophis toliapicus</i>
	<i>Palaeophis virginianus</i>
Order Crocodilia	
Family Gavialidae	
	<i>Eosuchus lerichei</i>
	<i>Thoracosaurus neocesariensis</i>
Family Alligatoridae	
	<i>Diplocynodon hantoniensis</i>

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The assemblage of reptiles found at the Fisher/Sullivan site is very unlike any modern North American assemblage. The presence of salt-water tolerant crocodilians and sea snakes (although boids rather than cobras) does, however, suggest the sort of faunal complexion that can be found today in the tropical marginal marine to marine coastal environments of the Indo-Pacific realm of southeast Asia and northern Australia. Therefore, in the early Eocene, the

coastal reptile fauna of the southeastern United States had much more similarity to the Eurasian Tethyan fauna (and its modern Indo-Pacific successor) than it does to American reptile faunas of today. This similarity is especially interesting in light of the strong similarity that the land flora from the Fisher/Sullivan site has with the existing flora of southeast Asia (see Part 8 in this volume).

The presence of a very diverse reptilian fauna in the Nanjemoy Formation suggests that the early Eocene coastal climate in Virginia, and along the southeastern seaboard of the United States, was much warmer and/or much more equable than it is today. The existence of three co-occurring genera of Eocene crocodilians in Virginia contrasts strikingly with the lesser diversity of crocodilians in the entirety of the southeastern United States today. Even in southern Florida, only two crocodilian genera co-occur today. Similarly, snakes fifteen to twenty feet in length are known today only in the tropical realm.

The size of the crocodilians *Thoracosaurus* and *Diplocynodon*, as well as the sea-going boids *Palaeophis toliapicus* and *Palaeophis virginianus*, readily place them at or near the top of the early Eocene marine to marginal marine food chain. During the early Eocene epoch of the Tertiary, there is no indication anywhere that mammals had begun to compete successfully with reptiles for the top carnivorous roles in the nektonic marine food chain. None of the known actinopterygian fishes appears to have been large enough to have competed directly with these reptiles, and only *Otodus obliquus* among the sharks seems likely to have offered serious competition. Therefore, reptiles continued to predominate among the top carnivorous niches of the oceanic food chain throughout Paleocene and early Eocene time, just as they had done during the Mesozoic.

## ACKNOWLEDGMENTS

I wish to thank all of the collectors, whose tireless efforts brought to light the reptile remains at the Fisher/Sullivan site, and whose generosity made these specimens available for study and/or donation. Similarly, I would like to thank landowners Mr. Dennis Fisher, Mr. Larry Fisher, and Mr. Russell Sullivan for making the site available for study and for permitting the most important specimens to be donated to the Smithsonian Institution. Thanks also are due to Jean Self-Trail of the U.S. Geological Survey for making it possible to have scanning electron microscope pictures of the teeth of *Parophisaurus mcclloskeyi*.

## BIBLIOGRAPHY

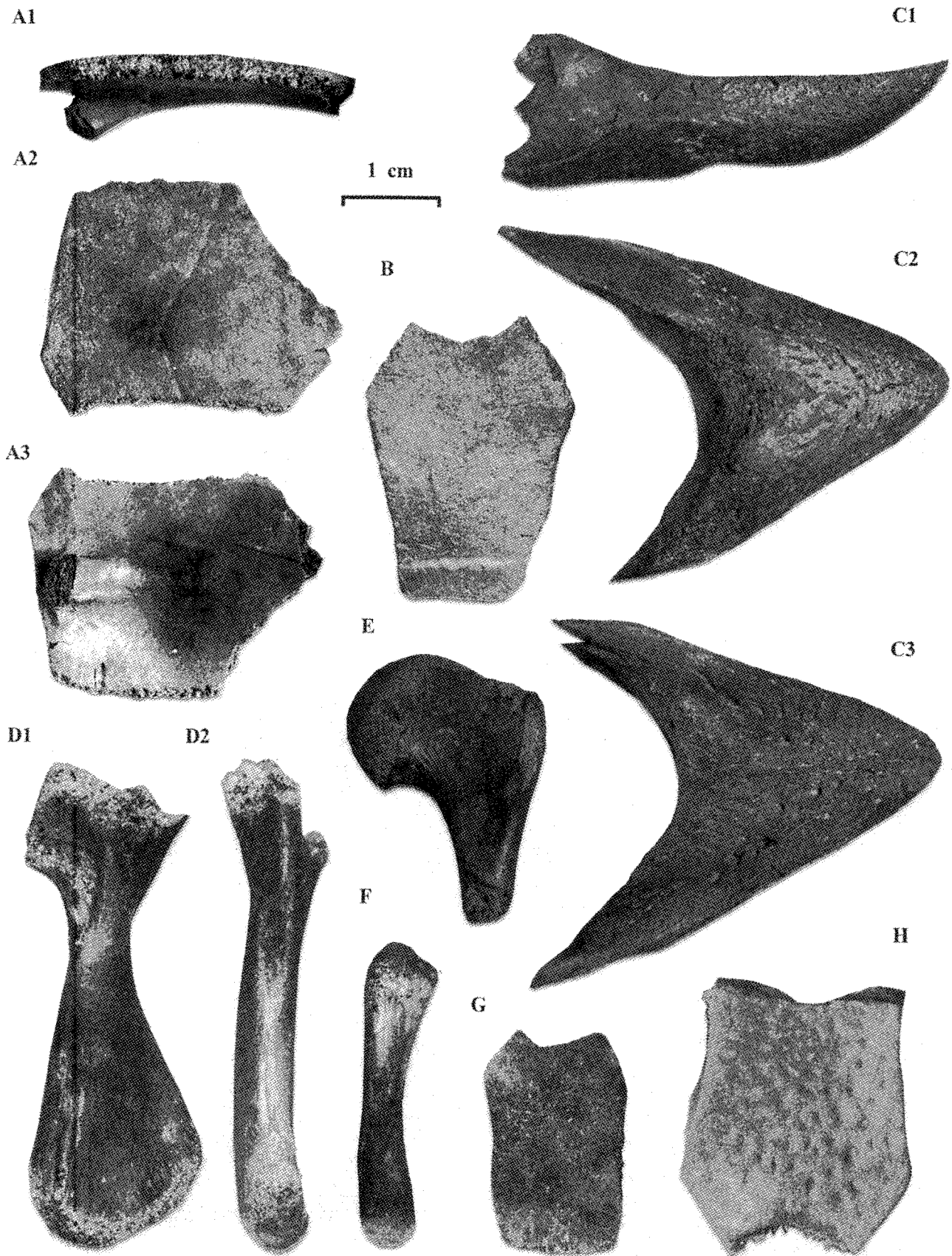
Barron, J.A., Larsen, B., Baldauf, J.G., and ODP 119 Scientific Party, 1989, Proximal and distal evidence of the history of the east Antarctic ice sheet; results from ODP leg 119: Abstracts of the Third International Conference on Palaeo-Oceanography, Blackwell, Oxford, p. 3.

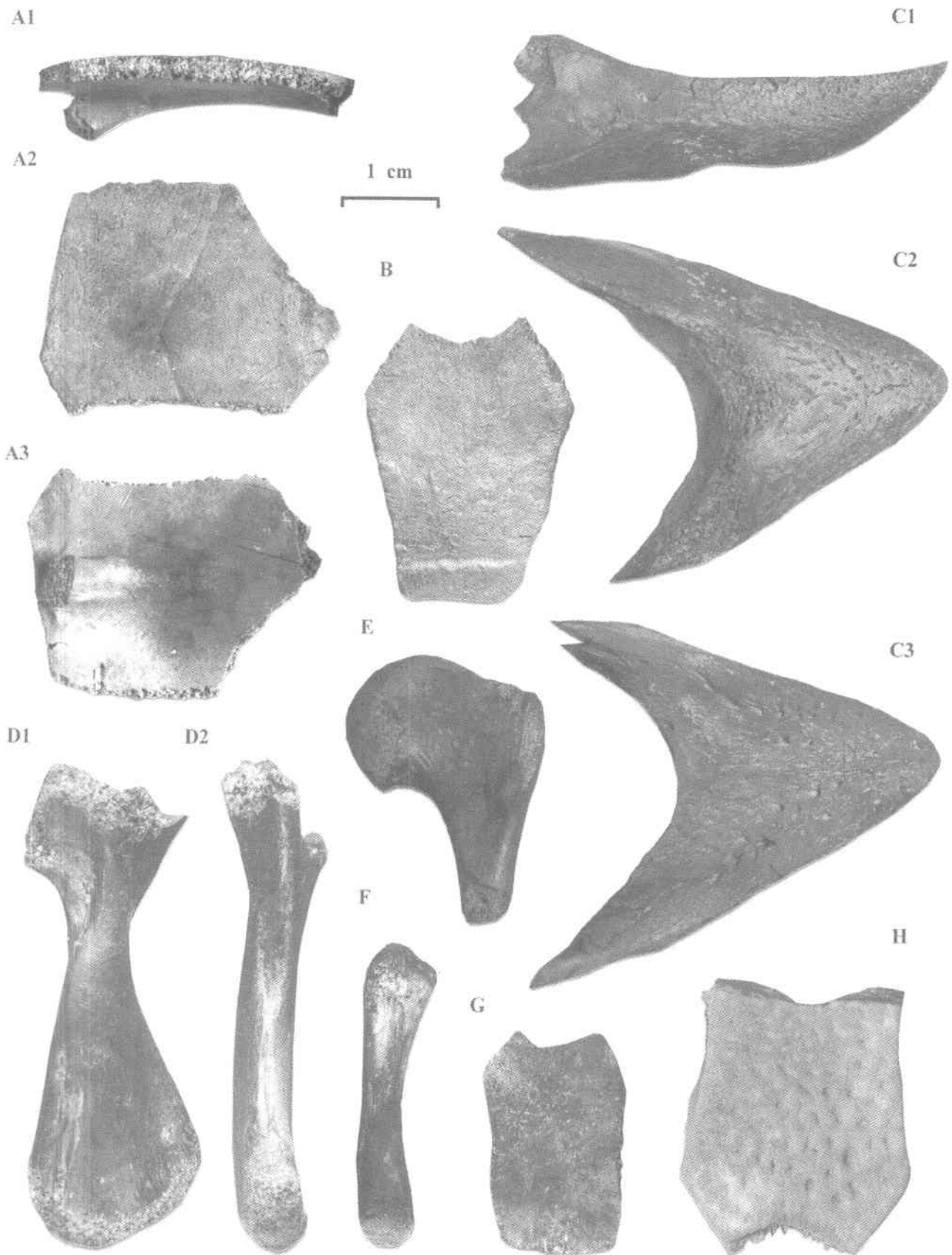
- Bauer, A.M., 1992, Lizards, in Cogger, H.G., and Zweifel, R.G., eds., Reptiles and Amphibians: New York, Smithmark Publishers Inc., p. 126-173.
- Benton, M.J., and Spencer, P.S., 1995, Fossil Reptiles of Great Britain: London, Chapman and Hall, 386 p.
- Blake, S.F., 1941, Note on a vertebra of *Palaeophis* from the Eocene of Maryland: Washington Academy of Sciences Journal 31:501-503.
- Brochu, C.A., 1997, Morphology, fossils, divergence timing, and the phylogenetic relationships of *Gavialis*: Systematic Biology, 46(3):479-522.
- Carpenter, Kenneth, 1983, *Thoracosaurus neocesariensis* (De Kay, 1842) (Crocodylia: Crocodylidae) from the Late Cretaceous Ripley Formation of Mississippi: Mississippi Geology 4(1):1-10.
- Casier, E., 1968, Les squelette cephalique de *Eocheilone brabantica* L. Dollo, du Bruxellien (Lutetien inferieur) de Belgique, et sa comparaison avec celui de *Chelone mydas* Linn: Bull. Inst. Roy. Sci. Nat. Belg.: 44(9):1-22.
- Cope, E.D., 1868, On some Cretaceous Reptilia: Philadelphia Academy of Natural Sciences Proceedings 20:233-242.
- Cope, E.D., 1869, Synopsis of the extinct Batrachia, Reptilia, and Aves of North America: Transactions of the American Philosophical Society 14:1-252.
- Dollo, Louis, 1907, Nouvelle note sur les reptiles de l'Eocène inférieur de la Belgique et des régions voisines (*Eosuchus lerichei* et *Eosphargis gigas*): Bull. Soc. Belge Géol., Proc.-verb. XXI, 81-85.
- Ehrmann, Werner, 1998, Implications of late Eocene to early Miocene clay mineral assemblages in McMurdo Sound (Ross Sea, Antarctica) on paleoclimate and ice dynamics: Palaeogeography, Palaeoclimatology, Palaeoecology 139:213-231.
- Estes, Richard, 1964, Fossil vertebrates from the Late Cretaceous Lance Formation, eastern Wyoming: University of California Publications in Geological Sciences, vol. 49, p. 1-180.
- Estes, Richard, 1983, Part 10 -- Sauria terrestria, Amphisbaenia, in, O. Kuhn, ed., Encyclopedia of Paleoherpétology: Stuttgart, Gustav Fischer Verlag, 249 p.
- Frakes, L.A., 1979, Climates through geologic time: Amsterdam, Elsevier, 310 pp.
- Hay, O.P., 1908, The Fossil Turtles of North America: Carnegie Institute of Washington, Publication 75:1-568.
- Holman, J.A., 1982, *Palaeophis casei*, new species, a tiny palaeophid snake from the early Eocene of Mississippi: Journal of Vertebrate Paleontology 2(2):163-166.
- Holman, J.A., and Case, G.R., 1988, Reptiles from the Eocene Tallahatta Formation of Alabama: Journal of Vertebrate Paleontology 8(3):328-333.
- Hutchison, J.H., 1980, Eocene lower vertebrates from Ellesmere Island, Canadian Arctic Archipelago, in Dawson, M.R., ed., Cenozoic history in and around the northern Atlantic and Arctic Oceans: Palaeogeography, Palaeoclimatology, Palaeoecology 30(3-4):325-347.
- Janensch, W. 1906, Über *Archaeophis proavus* Massalonge, eine Schlänge aus dem Eoçan des Monte Bolca: Beiträge zur Paläontologie von Österreich-Ungarns 19:1-33.
- Lynn, W.G., 1934, A new snake (*Paleophis virginianus*) from the Eocene of Virginia: Johns Hopkins University Studies in Geology 11:245-249.
- McDowell, S., and Bogert, C., 1954, The systematic position of *Lanthanotus* and the affinities of the anguimorph lizards: American Museum of Natural History Bulletin, vol. 105, p. 1-142.
- Miller, H.W., 1955, Some Eocene reptiles from New Jersey: Notula Naturae, Academy of Natural Sciences of Philadelphia 268:1-5.
- Moody, R.T.J., 1970, A revision of the taxonomy and morphology of certain Eocene Cheloniidae: University of London, PhD Dissertation, v. 1, p. 1-307.
- Moody, R.T.J., 1974, The taxonomy and morphology of *Puppigerus camperi* (Gray), an Eocene sea turtle from Northern Europe: Bulletin of the British Museum of Natural History (Geology) 25(2):155-186.
- Mook, C.C., 1960, *Diplocynodon* remains from the Bridger Beds of Wyoming: American Museum Novitates 2007:1-4.
- Müller, A.H., 1968, Lehrbuch der Paläozoologie: Band 3 - Vertebraten, Teil 2 -- Reptilien und Vogel: Jena, Gustav Fischer Verlag, 657 p.
- Norell, M.A., and Storrs, G.W., 1989, Catalogue and review of the type fossil crocodilians in the Yale Peabody Museum: Postilla 203:1-28.
- Olsen, S.J., 1968, Fish, amphibian, and reptile remains from archaeological sites, Part 1 -- Southeastern and southwestern United States, with an appendix on the osteology of the wild turkey: Papers of the Peabody Museum of Archaeology and Ethnology 556(2):1-137.
- Owen, Richard, 1841, Description of some Ophidiolites (*Palaeophis toliapicus*) from the London Clay at Sheppey, indicative of an extinct species of serpent: Transactions of the Geological Society of London 6:209-210.
- Owen, Richard, 1850, Monograph on the fossil reptilia of the London Clay, and of the Bracklesham and other Tertiary beds: Part 2 -- Crocodilia: London, The Palaeontographical Society.
- Parmley, Dennis, and Case, G.R., 1988, Palaeophid snakes from the Gulf coastal region of North America: Journal of Vertebrate Paleontology 8(3):334-339.

- Poe, Steven, 1996, Data set incongruence and the phylogeny of crocodilians: *Systematic Biology* 45(4):393-414.
- Rage, J.-C., 1984, Part 11 -- Serpentes, in O. Kuhn, ed., *Encyclopedia of Paleoherpétology*: Stuttgart, Gustav Fischer Verlag, 80 p.
- Rage, J.-C., and Wouters, G., 1979, Découverte du plus ancien Palaeopheide (Reptilia, Serpentes) dans le Maestrichtien du Maroc: *Géobios* 12(2):293-296.
- Shine, Richard, 1992, Snakes, in Cogger, H.G., and Zweifel, R.G., eds., *Reptiles and Amphibians*: New York, Smithmark Publishers Inc., p. 174-211.
- Steel, Rodney, 1973, Part 16 -- Crocodylia, in O. Kuhn, ed., *Encyclopedia of Paleoherpétology*: Stuttgart, Gustav Fischer Verlag, 116 p.
- Sullivan, R.M., 1982, Fossil lizards from Swain Quarry "Fort Union Formation," middle Paleocene (Torrejonian), Carbon County, Wyoming: *Journal of Paleontology*, vol. 56, no. 4, p. 996-1010.
- Sullivan, R.M., 1987, *Parophisaurus pawneensis* (Gilmore, 1928) new genus of anguid lizard from the middle Oligocene of North America: *Journal of Herpetology*, vol. 21, no. 2, p. 115-133.
- Swinton, W.E., 1937, The crocodile of Maransart (*Dollosuchus dixonii* [Owen]): *Mem. Mus. Roy. Hist. Nat. Belg.*, 80, 46 pp.
- Troedsson, G.T., 1924, On crocodilian remains from the Danian of Sweden: *Lunds Universitets Arsskrift*, N.F. 20(2):1-75.
- Weems, R.E., 1984, Vertebrate biozones of the Pamunkey Group (Paleocene and Eocene, Maryland and Virginia): in Ward, L.W., and Krafft, Kathleen, eds., *Stratigraphy and paleontology of the outcropping Tertiary beds in the Pamunkey River region, central Virginia Coastal Plain: Guidebook for Atlantic Coastal Plain Geological Association 1984 field trip*, p.198-204.
- Weems, R.E., 1988, Paleocene turtles from the Aquia and Brightseat Formations, with a discussion of their bearing on sea turtle evolution and phylogeny: *Proceedings of the Biological Society of Washington* 101(1):109-145.

#### Plate 5.1.

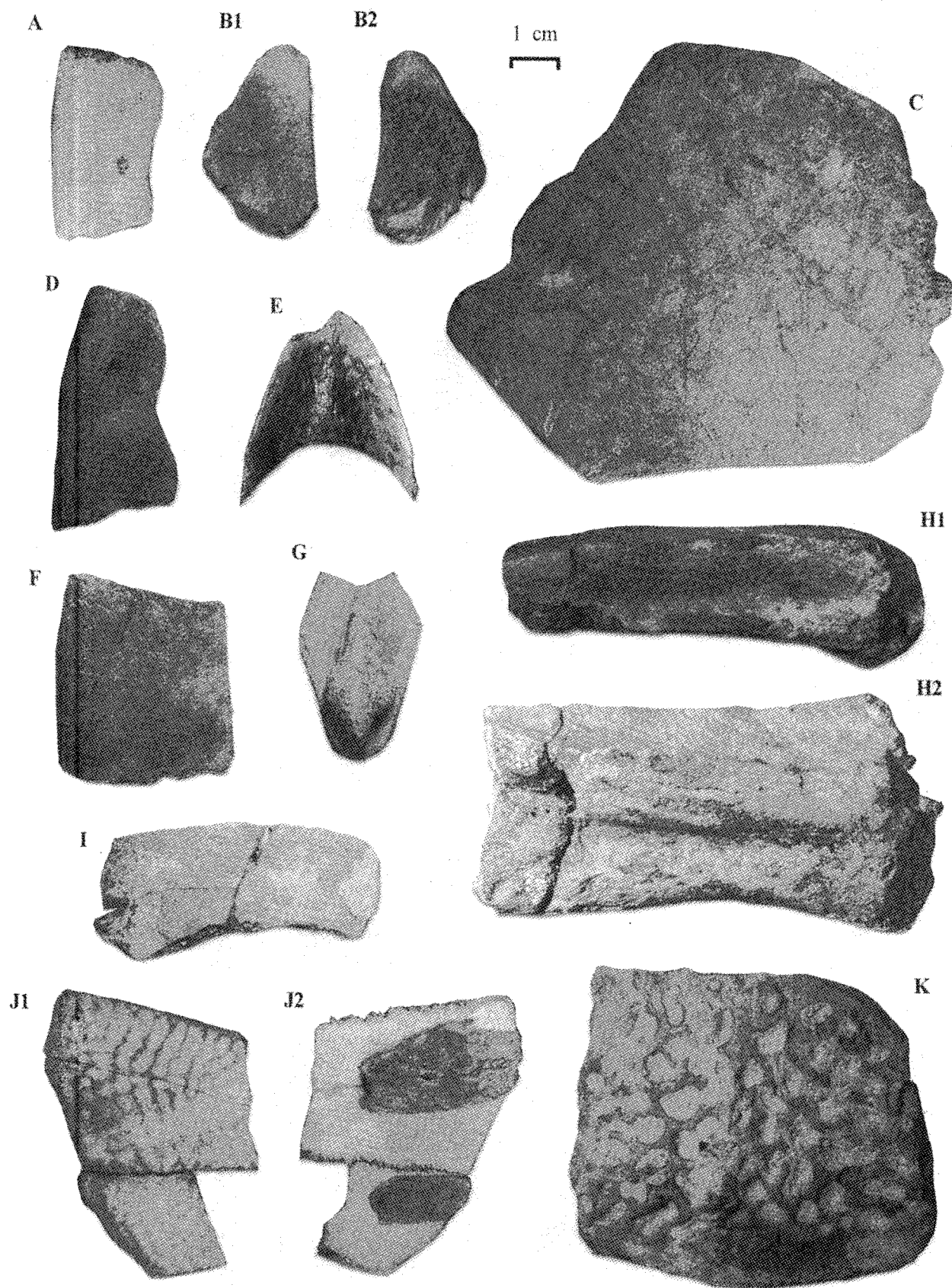
- A. *Puppigerus camperi*, proximal portion of costal element in side (A1), dorsal (A2), and ventral (A3) views, Parks collection.
- B. *Puppigerus camperi*, neural element in dorsal view, Parks collection.
- C. *Puppigerus camperi*, fused dentaries in oral (C1), lateral (C2), and aboral (C3) views, Parks collection.
- D. *Puppigerus camperi*, left humerus in dorsal (D1) and lateral (D2) views, Parks collection.
- E. *Puppigerus camperi*, proximal portion of femur in lateral view, Folmer collection.
- F. *Puppigerus camperi*, ulna, Parks collection.
- G. *Puppigerus camperi*, first neural element in dorsal view, Parks collection.
- H. cf. *Trionyx pennatus* (USNM 496195), neural element in dorsal view, Keil collection.

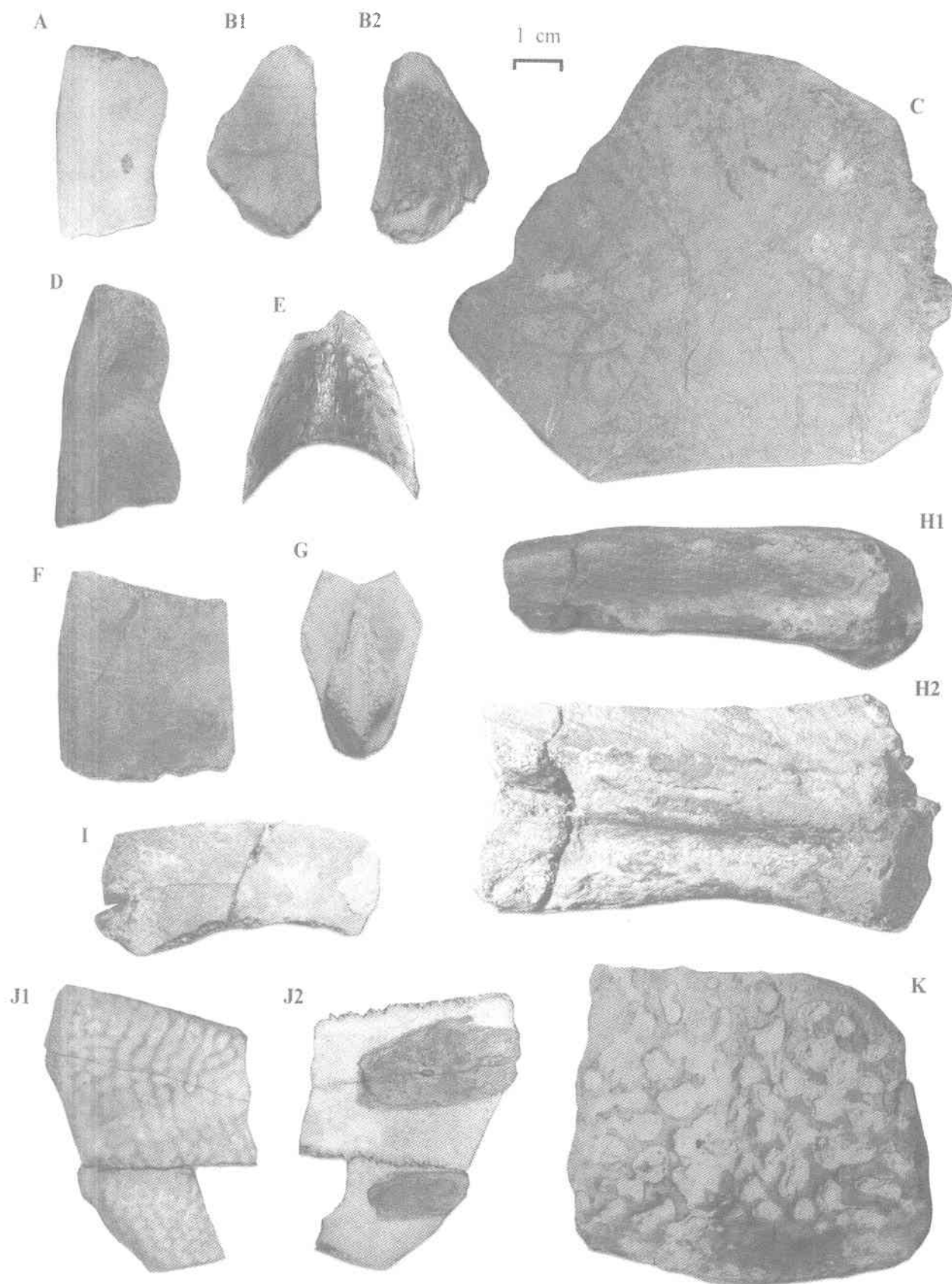




**Plate 5.2.**

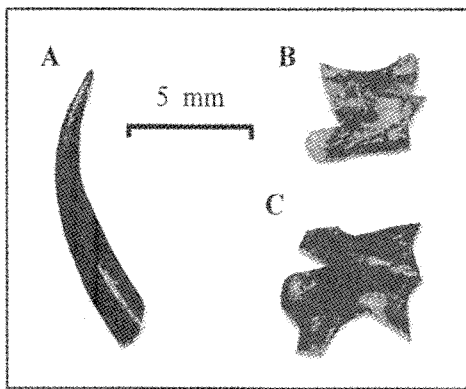
- A. *Puppigerus camperi*, peripheral element (USNM 496191), Folmer collection.
- B. cf. *Eosphargis gigas*, frontal element (USNM 496196) in dorsal (B1) and ventral (B2) views, Folmer collection.
- C. ?*Dollochelys* sp., fragment of plastron (USNM 496193), Folmer collection.
- D. *Puppigerus camperi*, peripheral element (USNM 496187), Folmer collection.
- E. *Puppigerus camperi*, fused dentaries (USNM 496190) in oral view, Keil collection.
- F. *Puppigerus camperi*, peripheral element (USNM 496182), Folmer collection.
- G. *Puppigerus camperi*, neural element (USNM 496189) in ventral view, Folmer collection.
- H. ?*Dollochelys* sp., fragment of left dentary (USNM 496192) in oral (H1) and internal (H2) view, Keil collection.
- I. *Puppigerus camperi*, left costal element (USNM 496177) in dorsal view, Folmer collection.
- J. cf. *Trionyx pennatus*, distal portions of left sixth and seventh costals (USNM 496194), Folmer collection.
- K. *Diplocynodon hantoniensis*?, dermal armor, Keil collection.



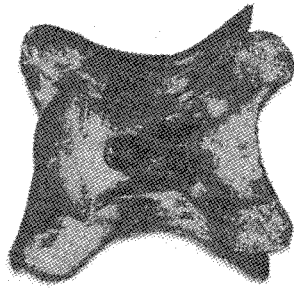


**Plate 5.3.**

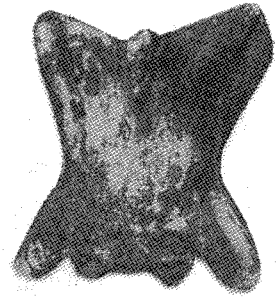
- A. *Palaeophis toliapicus*?, tooth (USNM 496205), Folmer collection.
- B. *Palaeophis casei*, trunk vertebra (USNM 496197), Folmer collection.
- C. *Palaeophis toliapicus*, caudal vertebra (USNM 496200), Folmer collection.
- D. *Palaeophis toliapicus*, trunk vertebra (USNM 496202) in ventral (D1), dorsal (D2), posterior (D3), right lateral (D4), and anterior (D5) views, Folmer collection.
- E. *Diplocynodon hantoniensis*, tooth (USNM 496207) in internal (E1) and lateral (E2) view, Harding collection.
- F. *Thoracosaurus neocesariensis*, lateral tooth (USNM 496208) in lateral (F1) and basal (F2) views, Bennett collection.
- G. *Eosuchus lerichei*, anterior tooth in lateral (G1) and basal (G2) views, Parks collection.
- H. *Eosuchus lerichei*, posterior tooth in internal (H1) and basal (H2) views, Parks collection.
- I. *Eosuchus lerichei*, dermal armor (USNM 496211), Savia collection.



D1



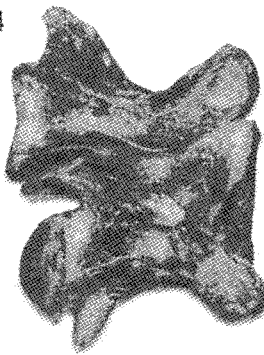
D2



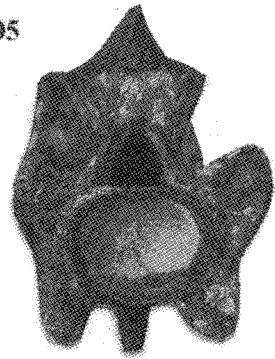
D3



D4



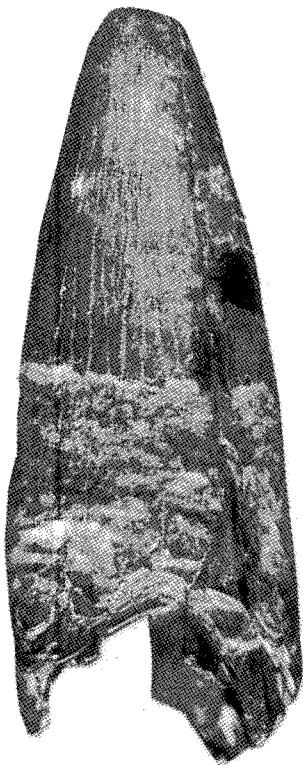
D5



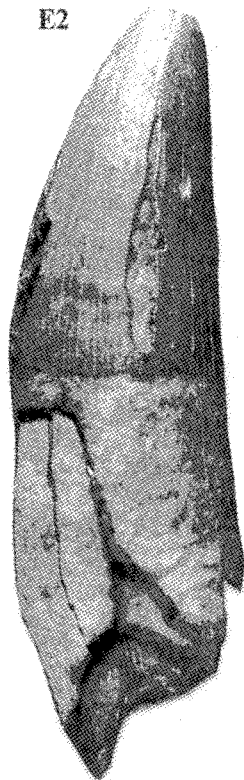
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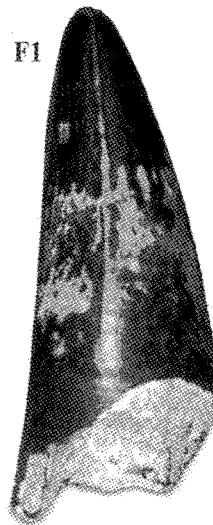
E1



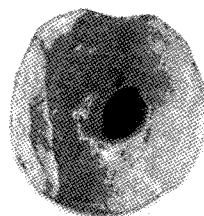
E2



F1



F2



G1



G2



H1

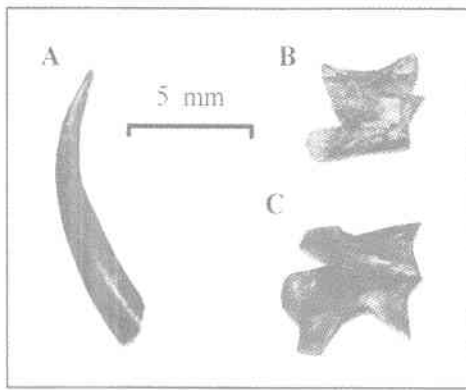


H2

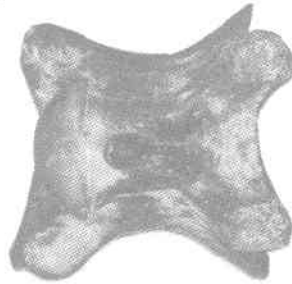


I





D1



D2



D3



D4



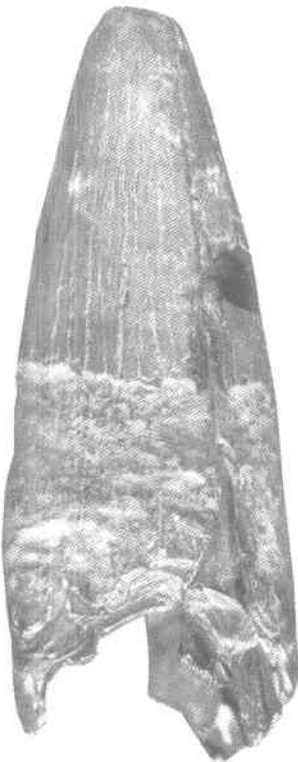
D5



1 cm



E1



E2



F1



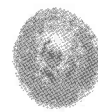
F2



G1



G2



H1



H2

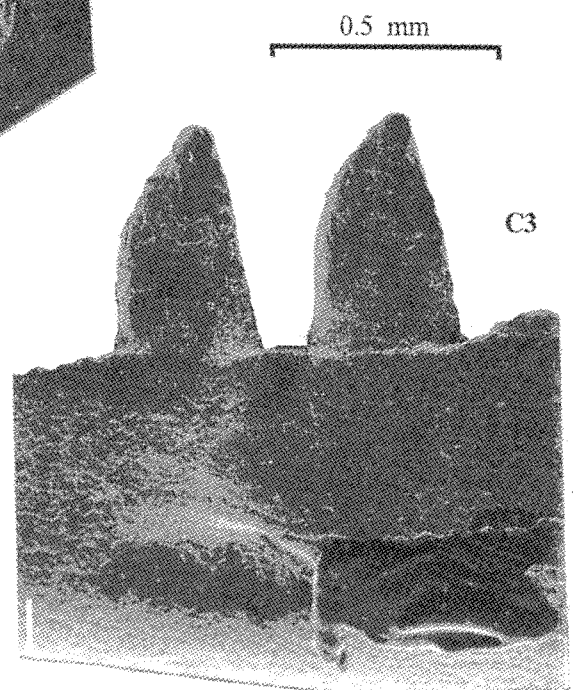
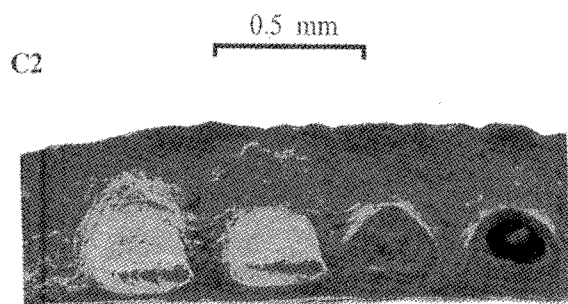
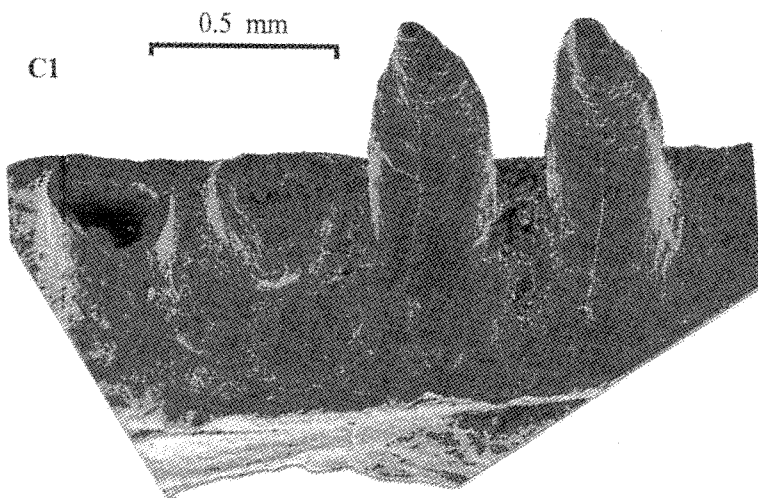
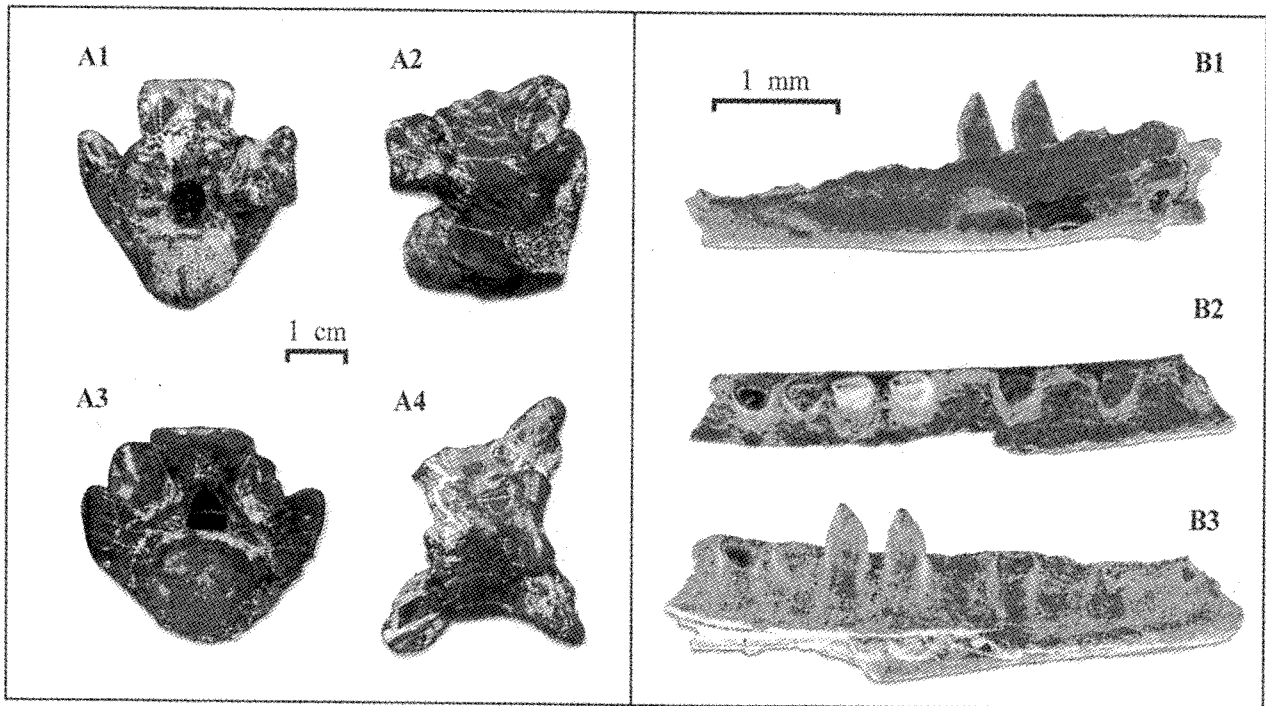


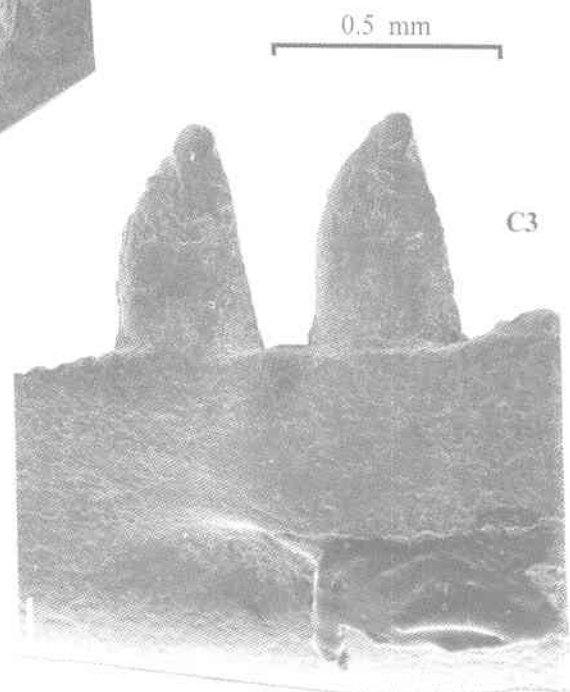
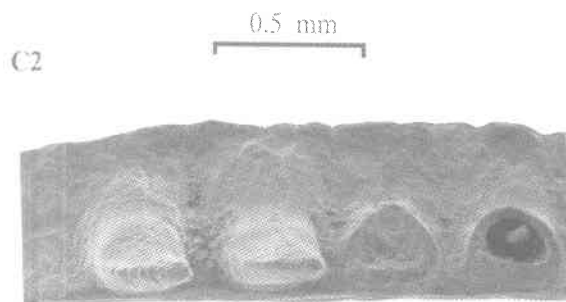
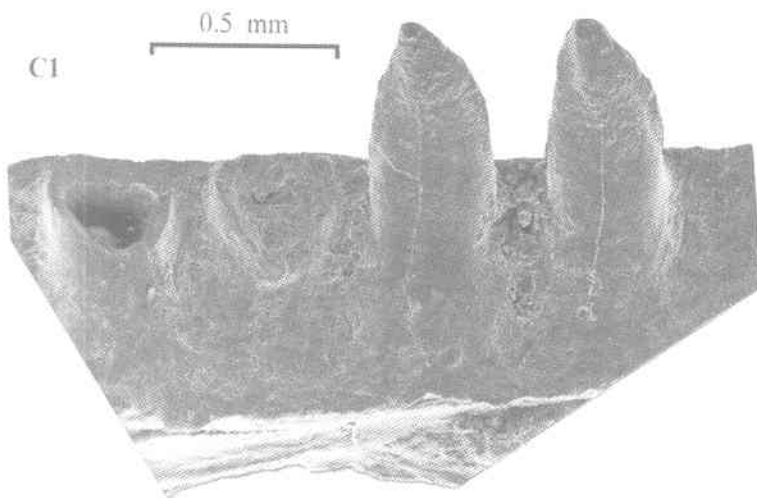
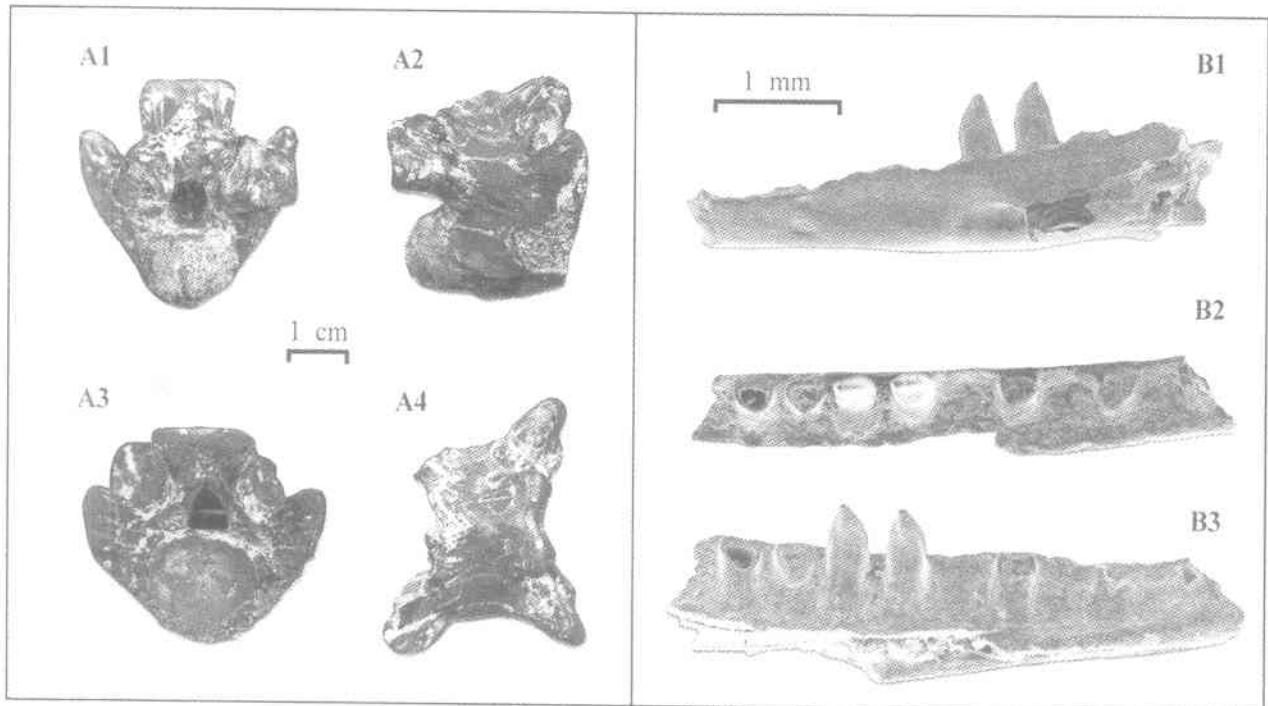
I



**Plate 5.4**

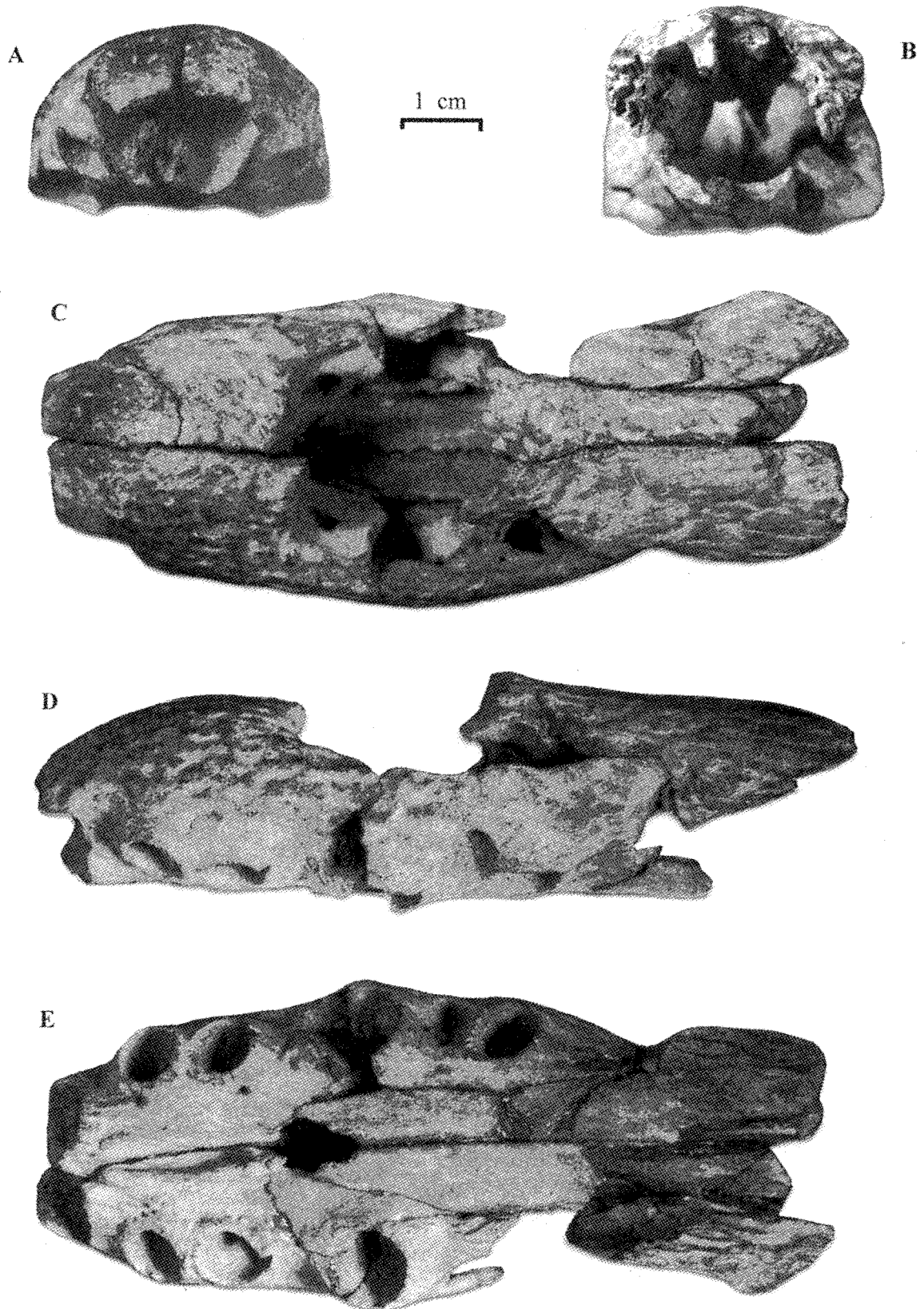
- A. *Palaeophis virginianus*, vertebra (USNM 494368) in posterior (A1), lateral (A2), anterior (A3), and dorsal (A4) views, Keil collection.
- B. *Parophisaurus mccloskeyi*, left dentary (USNM 498662) in external (B1), oral (B2), and internal (B3) views, McCloskey collection.
- C. *Parophisaurus mccloskeyi*, teeth in left dentary in internal-oblique (C1), oral (C2), and external (C3) view, McCloskey collection.

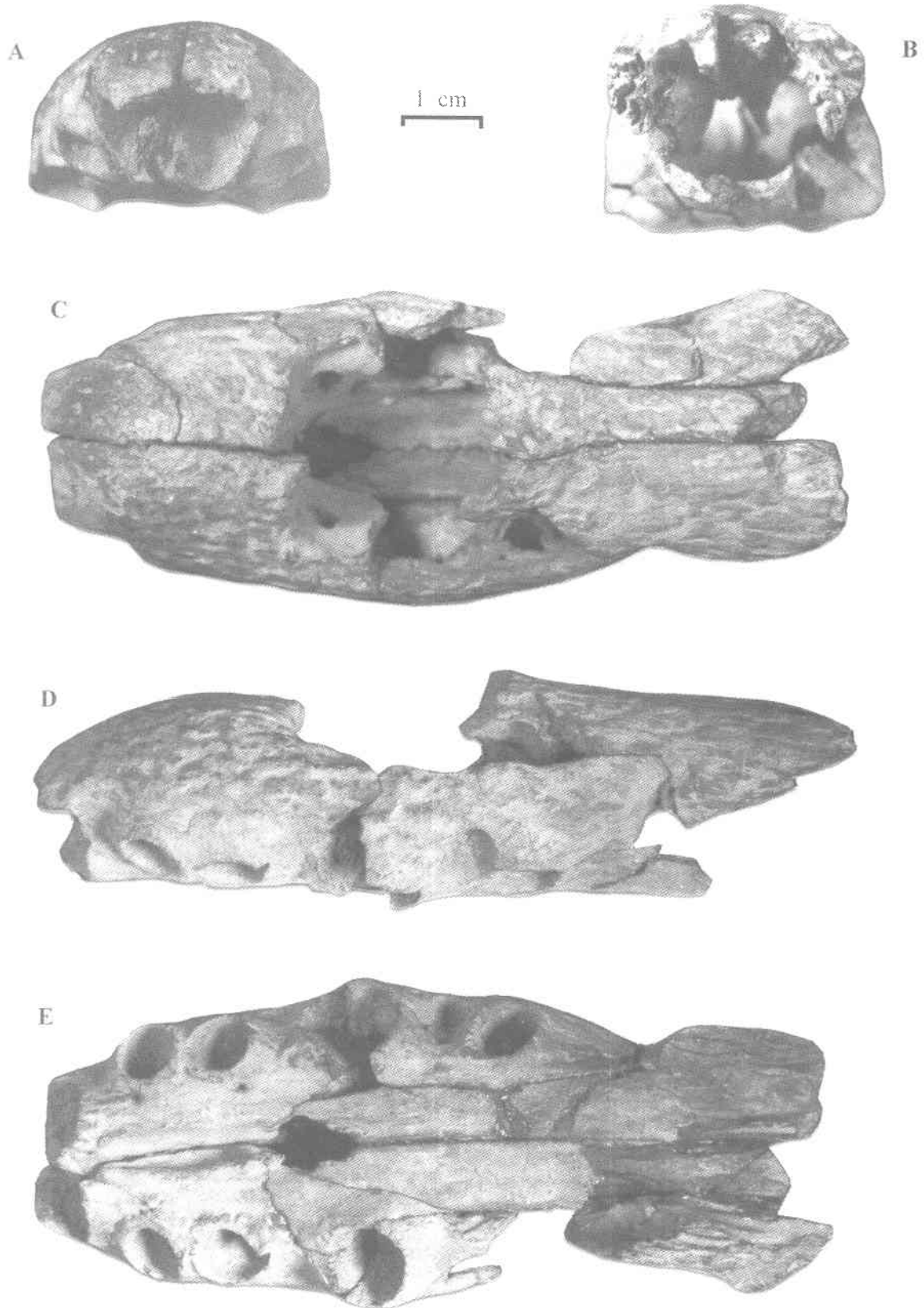




**Plate 5.5**

*Eosuchus lerichei*, premaxillaries (USNM 498862) in anterior (A), posterior (B), dorsal (C), left lateral (D), and ventral (E) views, Ison collection.







## Part 6. Early Eocene Birds from Eastern North America: A Faunule from the Nanjemoy Formation of Virginia

Storrs L. Olson

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Smithsonian Institution, Washington, D.C. 20560*

### ABSTRACT

Fossil bird remains from the Fisher/Sullivan Site, Stafford County, Virginia, come from marine sediments of the Potapaco Member of the early Eocene Nanjemoy Formation and are equivalent in age to the London Clay of southeastern England, which has produced many fossil birds. The 33 specimens from the Fisher/Sullivan Site are referable to at least 11 species and constitute the first early Eocene avifauna known from eastern North America. The taxa represented include a pseudodontorn (Pelagornithidae); various shorebird-like species, some with similarities to the Burhinidae, Rostratulidae, and Phoenicopteridae; and three species of Caprimulgiformes/Apodiformes. Only the pseudodontorn was pelagic, all the other being shore or land birds, which suggests rather unusual depositional circumstances.

### INTRODUCTION

The earliest part of the Tertiary was a critical time in the origin of orders and families of modern birds. This was a period when birds were diversifying rapidly and were making many evolutionary experiments in response to the new regimes of climate and vegetation that appeared after the end of the Cretaceous. Our knowledge of birds of this age comes mainly from two geographic areas---western North America and western Europe, especially England. In the American west, particularly Wyoming, very fragmentary and minimally informative bird remains have long been known from Paleocene and early Eocene mudstones that have been so thoroughly prospected for mammalian teeth (e.g., Gingerich, 1980). From many of the same deposits, excellent material of fossil birds has been found in recent years in freshwater limestone nodules (e.g., Houde, 1988; Houde and Olson, 1989; 1992). Another prime source of birds of this age has been the lacustrine deposits of the Green River Formation (e.g., Olson, 1987).

On the eastern side of the Atlantic, the beds of the early Eocene London Clay have produced fossil birds in great number, the very best originating in the mudflats at Walton-on-the-Naze in Essex. Most of these are in a private collection and have not been documented in the scientific literature. Although there is a rich Neogene record of birds in eastern North America, fossils of early Paleogene age are quite scarce, consisting mainly of a few Paleocene fossils from Maryland and Virginia (Olson, 1994), and a single toe bone of *Diatryma* from the Lower Eocene of New Jersey (Andors, 1988:42-44).

Recently, however, an intriguing faunule consisting of

33 specimens belonging to at least 11 species of birds offers a first glimpse into the birdlife of eastern North America in the early Eocene. These come from sediments of the Potapaco Member of the Nanjemoy Formation of the early Tertiary Pamunkey Group that are exposed in the bed of an unnamed tributary of Muddy Creek, north of Virginia State Highway 3, in Stafford County, east of Fredericksburg, Virginia. The age of the deposit is early Eocene, corresponding to the early part of calcareous nannoplankton Zone NP 11, and overlaps broadly in age with the London Clay (for details of the geology and paleoecology of this site, termed the Fisher/Sullivan Site, see Weems and Grimsley, Part 1, and other papers in this volume). The fossils were deposited in a nearshore marine environment and were recovered by quarrying the sediment and washing it through screens. The specimens have been cataloged in the collections of the Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D. C. (acronym USNM). Identifications were based on comparisons with modern skeletal material housed in the collections of the Division of Birds, Department of Vertebrate Zoology, of the same institution.

### SYSTEMATIC PALEONTOLOGY

#### **Pelecaniformes**

#### **Pelagornithidae**

#### *Odontopteryx?* sp.

**Material:** Carpometacarpus, left proximal end lacking most of the alular metacarpal, USNM 496364 (Fig. 1a,b). Collected by Mike Folmer. Width and depth of carpal trochlea, 12.5 X 18.0 mm.

Carpometacarpus, left distal end, USNM 496417 (Fig. 1c,d). Collected by Mike Folmer. Width and depth of articular surface, 10.7 X 14.7 mm. This is quite conceivably from one and the same bone as the proximal fragment.

Pedal digit III, phalanx 1, proximal half, USNM 496365 (Fig. 1e,f). Collected by Mike Folmer. Width and depth of proximal articulation, 9.5 X 9.8 mm. The precise bone of the foot represented by this fragment is only a guess.

**Discussion:** These bones come from a bird about the size of the Peruvian Brown Pelican, *Pelecanus thagus*. The very large pseudotoothed birds of the family Pelagornithidae range in age from Paleocene to relatively late in the Neogene (Olson, 1985). A much needed revision of the complexities of this group has been initiated by K. I.

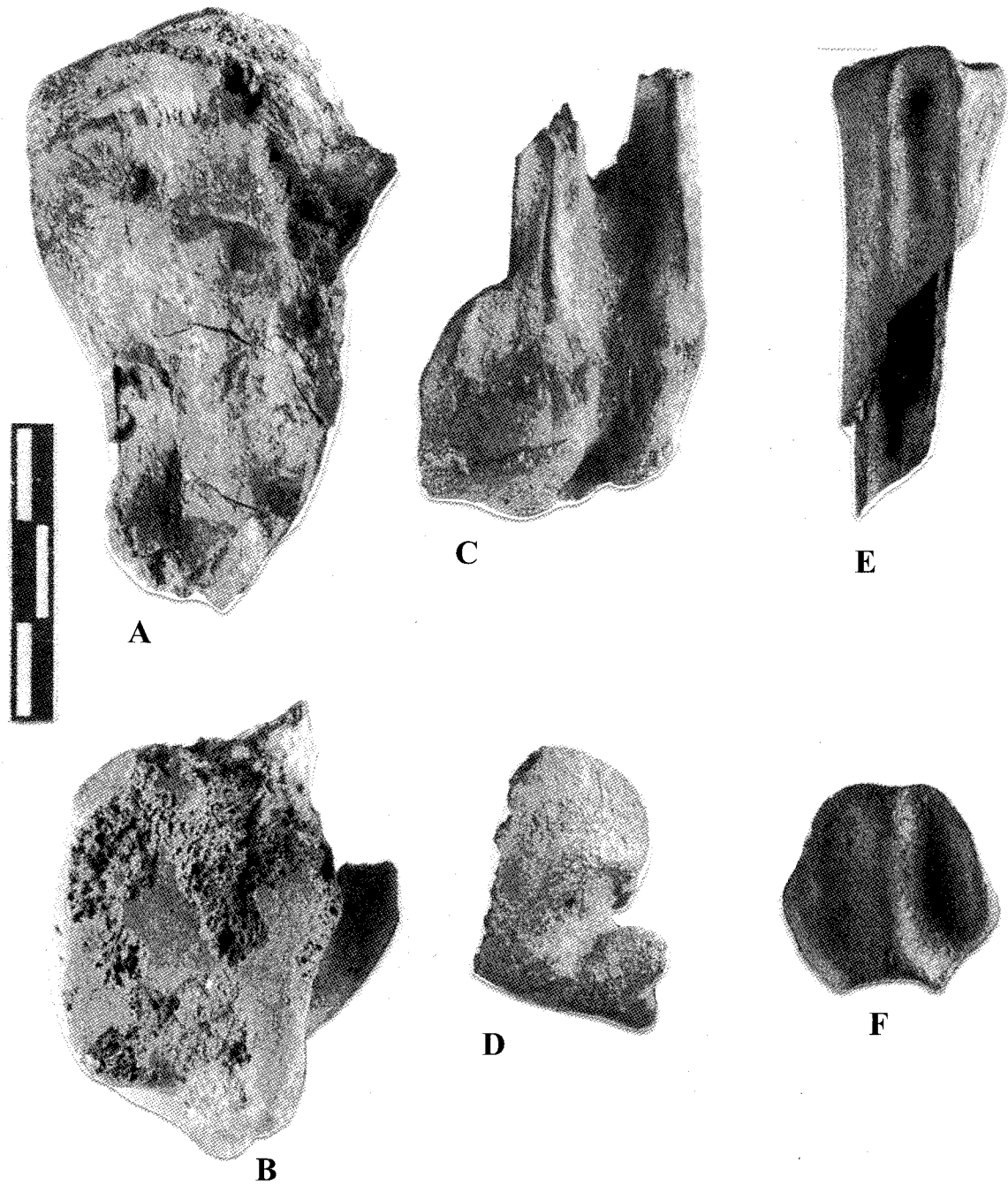


Figure 1. *Odontopteryx?* sp.: A, carpometacarpus, left proximal end lacking most of the alular metacarpal, USNM 496364 (internal view); B, same, proximal view; C, carpometacarpus, left distal end, USNM 496417 (external view); D, same, distal view; E, pedal digit III, phalanx 1, proximal half, USNM 496365 (ventral view); F, same, proximal view. Scale is in 0.5 cm increments.

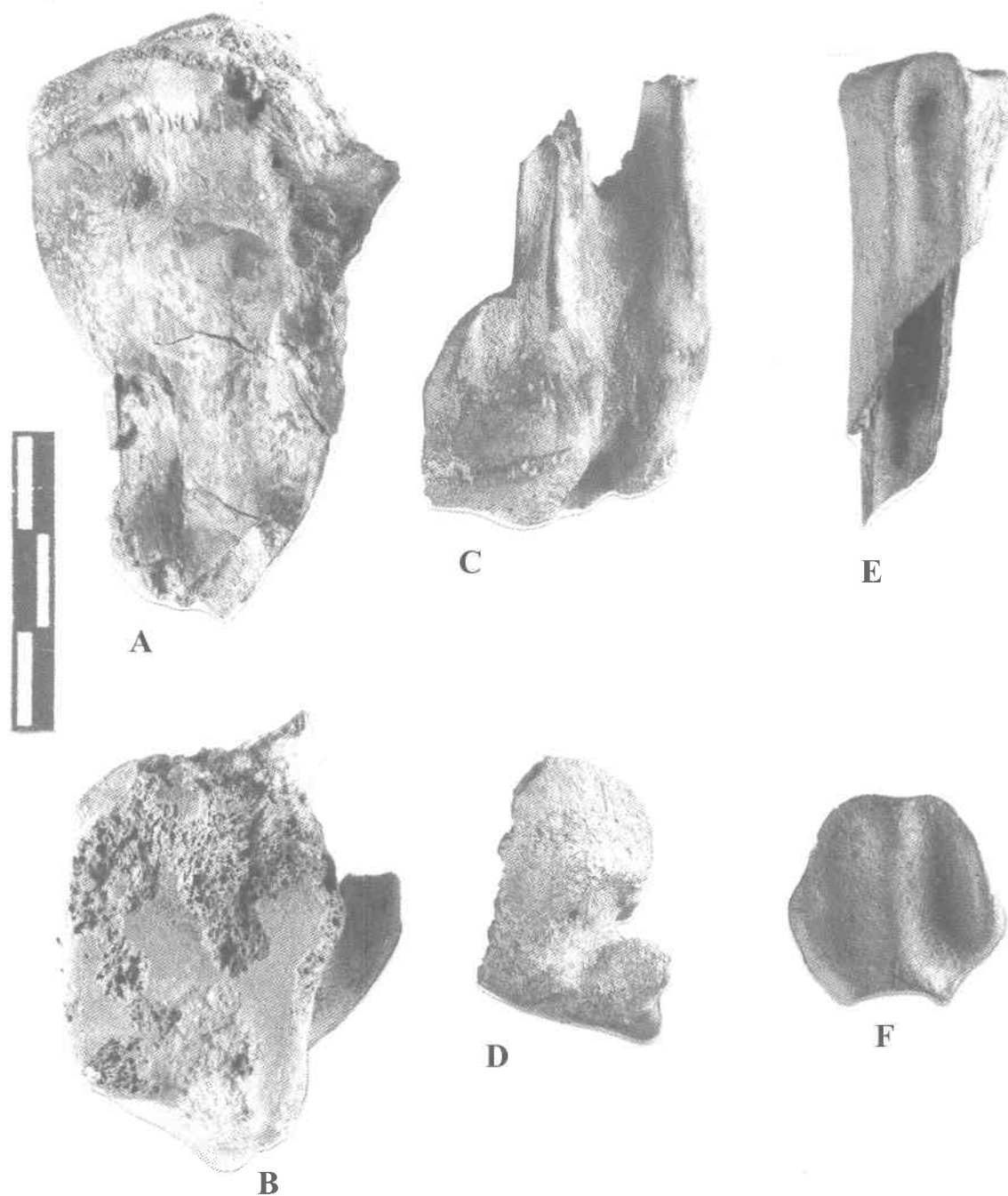


Figure 1. *Odontopteryx?* sp.: A, carpometacarpus, left proximal end lacking most of the alular metacarpal, USNM 496364 (internal view); B, same, proximal view; C, carpometacarpus, left distal end, USNM 496417 (external view); D, same, distal view; E, pedal digit III, phalanx 1, proximal half, USNM 496365 (ventral view); F, same, proximal view. Scale is in 0.5 cm increments.

Warheit and Olson but is still far from completion. At least two species differing in size are known from the London Clay, for which there are numerous names available, the oldest being *Odontopteryx toliapica* Owen, a species that was smaller than the one indicated by the Nanjemoy bones.

The Eocene pseudodontornis were more primitive and differed considerably from the species known from the late Oligocene onward, most of which are referable to the genus *Pelagornis* Lartet. The carpometacarpus from the Fisher/Sullivan Site differs from a specimen from the late Oligocene of South Carolina in having the trochlea in proximal view higher and narrower (Fig. 1b). The two were similar, however, in the flattened rather than rounded trailing edge of the trochlea.

### Charadriiformes Graculavidae?

genus and species indeterminate #1

**Material:** Scapula, left, worn and lacking posterior third, USNM 496367 (Fig. 2d). Collected by Tom Parks. Shaft width posterior to articular expansion, 4.3 mm.

Coracoid, left shaft, USNM 496368 (Fig. 2e). Collected by Mike Folmer. Shaft width and depth at midpoint, 4.6 X 3.6 mm.

Humerus, left distal condyles, USNM 496369 (Fig. 2c). Collected by Gary Grimsley. Depth through radial condyle, 8.5 mm.

Ulna, right proximal end, USNM 496370 (Fig. 2a). Collected by Dick Grier, Jr. Proximal width and depth, 8.6 X 9.2 mm. A piece of shaft (USNM 496371) collected independently by Ron Keil appears as if it may have come from the same specimen, although there is no point of contact between the two.

Tibiotarsus, left distal third lacking condyles, USNM 496366 (Fig. 2b). Collected by Richard Brezina. Width at proximal opening of tendinal canal, 8.0 mm; width and depth of shaft approximately one-third the length from the distal end, 4.7 X 4.4 mm.

**Discussion:** Olson and Parris (1987) used the name Graculavidae as a form family to encompass various late Cretaceous/early Tertiary taxa based on fragmentary material showing similarities to basal "charadriiforms" such as the Burhinidae, and to *Presbyornis*, a primitive waterfowl (Anseriformes). It is a convenient catch-all, intended as such, members of which will presumably be removed to their correct families as their anatomy becomes better known (e.g., Olson, in press).

The tibiotarsus listed above (Fig. 2b) is very similar in size and overall morphology to that of the Australian Bush Stone-curlew, *Burhinus magnirostris*, and hence a good candidate for referral to the Graculavidae. Per Ericson (Swedish Museum of Natural History, Stockholm, personal communication) examined it and was convinced that it was not referable to *Presbyornis*. It differs from

*Palaeotringa* Marsh, and *Dakotornis* Erickson, in lacking a foramen in the groove for the tendon of *M. peroneus brevis* (Olson and Parris, 1987). The other elements (Fig. 2a, c-e), though very scrappy, would be compatible with a bird of this size and general structure.



Figure 2. Graculavidae?, genus and species indeterminate #1: A, ulna, right proximal end, USNM 496370 (internal view), with possibly associated piece of shaft, USNM 496371; B, tibiotarsus, left distal third lacking condyles, USNM 496366 (anterior view); C, humerus, left distal condyles, USNM 496369 (palmar view); D, scapula, left, worn and lacking posterior third, USNM 496367 (dorsal view); E, coracoid, left shaft, USNM 496368 (ventral view). Scale is in 0.5 cm increments.

genus and species indeterminate #2

**Material:** Ulna, right distal end, USNM 496372 (Fig. 3a). Collected by Ron Keil. Distal width and depth, 5.9 X 5.4 mm.

Carpometacarpus, right distal symphysis, USNM 496373 (Fig. 3b). Collected by Mike Folmer. Distal width

Warheit and Olson but is still far from completion. At least two species differing in size are known from the London Clay, for which there are numerous names available, the oldest being *Odontopteryx toliapica* Owen, a species that was smaller than the one indicated by the Nanjemoy bones.

The Eocene pseudodontorns were more primitive and differed considerably from the species known from the late Oligocene onward, most of which are referable to the genus *Pelagornis* Lartet. The carpometacarpus from the Fisher/Sullivan Site differs from a specimen from the late Oligocene of South Carolina in having the trochlea in proximal view higher and narrower (Fig. 1b). The two were similar, however, in the flattened rather than rounded trailing edge of the trochlea.

### Charadriiformes Graculavidae?

genus and species indeterminate #1

**Material:** Scapula, left, worn and lacking posterior third, USNM 496367 (Fig. 2d). Collected by Tom Parks. Shaft width posterior to articular expansion, 4.3 mm.

Coracoid, left shaft, USNM 496368 (Fig. 2e). Collected by Mike Folmer. Shaft width and depth at midpoint, 4.6 X 3.6 mm.

Humerus, left distal condyles, USNM 496369 (Fig. 2c). Collected by Gary Grimsley. Depth through radial condyle, 8.5 mm.

Ulna, right proximal end, USNM 496370 (Fig. 2a). Collected by Dick Grier, Jr. Proximal width and depth, 8.6 X 9.2 mm. A piece of shaft (USNM 496371) collected independently by Ron Keil appears as if it may have come from the same specimen, although there is no point of contact between the two.

Tibiotarsus, left distal third lacking condyles, USNM 496366 (Fig. 2b). Collected by Richard Brezina. Width at proximal opening of tendinal canal, 8.0 mm; width and depth of shaft approximately one-third the length from the distal end, 4.7 X 4.4 mm.

**Discussion:** Olson and Parris (1987) used the name Graculavidae as a form family to encompass various late Cretaceous/early Tertiary taxa based on fragmentary material showing similarities to basal "charadriiforms" such as the Burhinidae, and to *Presbyornis*, a primitive waterfowl (Anseriformes). It is a convenient catch-all, intended as such, members of which will presumably be removed to their correct families as their anatomy becomes better known (e.g., Olson, in press).

The tibiotarsus listed above (Fig. 2b) is very similar in size and overall morphology to that of the Australian Bush Stone-curlew, *Burhinus magnirostris*, and hence a good candidate for referral to the Graculavidae. Per Ericson (Swedish Museum of Natural History, Stockholm, personal communication) examined it and was convinced that it was not referable to *Presbyornis*. It differs from

*Palaeotringa* Marsh, and *Dakotornis* Erickson, in lacking a foramen in the groove for the tendon of *M. peroneus brevis* (Olson and Parris, 1987). The other elements (Fig. 2a, c-e), though very scrappy, would be compatible with a bird of this size and general structure.

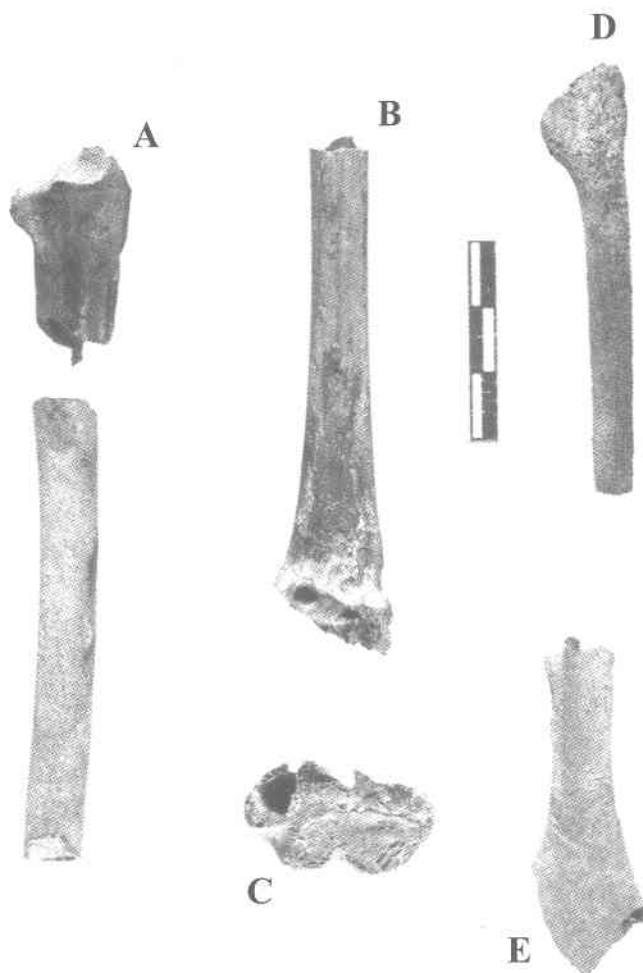


Figure 2. Graculavidae?, genus and species indeterminate #1: A, ulna, right proximal end, USNM 496370 (internal view), with possibly associated piece of shaft, USNM 496371; B, tibiotarsus, left distal third lacking condyles, USNM 496366 (anterior view); C, humerus, left distal condyles, USNM 496369 (palmar view); D, scapula, left, worn and lacking posterior third, USNM 496367 (dorsal view); E, coracoid, left shaft, USNM 496368 (ventral view). Scale is in 0.5 cm increments.

genus and species indeterminate #2

**Material:** Ulna, right distal end, USNM 496372 (Fig. 3a). Collected by Ron Keil. Distal width and depth, 5.9 X 5.4 mm.

Carpometacarpus, right distal symphysis, USNM 496373 (Fig. 3b). Collected by Mike Folmer. Distal width

and depth, 3.7 X 4.8 mm.

**Discussion:** These are from a bird the size of the Old World Stone-curlew, *Burhinus oediconemus*, to which the carpometacarpus bears some resemblance, although the ulna lacks the deep ligamental pit on the dorsal surface seen in the modern bird. They are here tentatively included as a smaller species of Graculavidae.

### Scolopaci

family, genus, and species indeterminate

**Material:** Humerus, right distal end lacking condyles, USNM 496374 (Fig. 3c). Collected by Tom Parks. Width just above ectepicondylar spur, 4.1 mm; width and depth of

shaft at approximate midpoint, 3.0 X 2.3 mm.

Tarsometatarsus, right distal end, USNM 496375 (Fig. 3d). Collected by Tom Parks. Distal width, 5.0 mm; width through outer and middle trochleae, 3.8 mm.

Pedal phalanx, probably phalanx 1 digit III, USNM 496376 (Fig. 3e). Collected by Mark Bennett. Length, 12.0 mm.

**Discussion:** These elements would all be compatible with a shorebird intermediate in size between the Old World and New World painted snipes (*Rostratula benghalensis* and *R. semicollaris*). The tarsometatarsus and humerus are clearly from some sort of limicoline charadriiform and the former compares better with the Rostratulidae than with the more derived families Scolopacidae and Charadriidae. The

humerus differs considerably from that of *Rostratula*, however, in the much deeper brachial depression and the better development of the area where the ectepicondylar spur arises. I would not have attempted to identify the toe bone but it is exactly of the size expected for the species represented by the other two bones and is very similar to phalanx 1 digit III in *Rostratula*. The Rostratulidae and Jacanidae are early offshoots of the suborder Scolopaci. Shorebirds apparently having some affinity with these two families are also known in the London Clay.

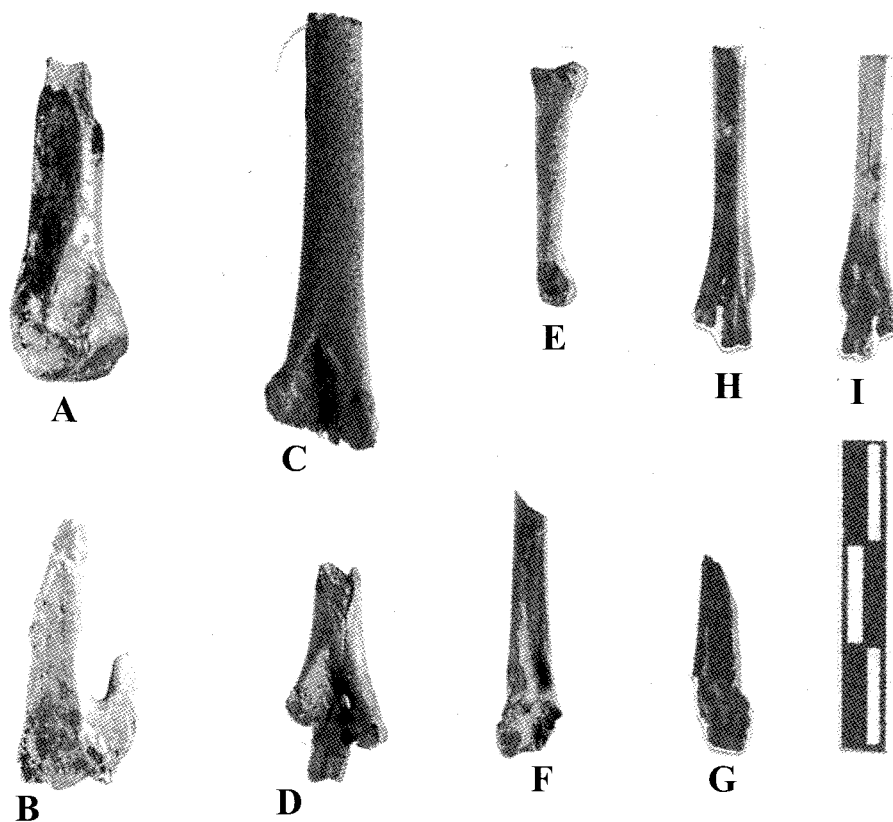


Figure 3. Various shorebird-like taxa. Graculavidae, genus and species indeterminate #2 : A, ulna, right distal end, USNM 496372 (internal view); B, carpometacarpus, right distal symphysis, USNM 496373 (internal view). Scolopaci, family, genus, and species indeterminate: C, humerus, right distal end lacking condyles, USNM 496374 (palmar view); D, tarsometatarsus, right distal end, USNM 496375 (posterior view); E, pedal phalanx, probably phalanx 1 digit III, USNM 496376 (lateral view). cf. *Coturnipes cooperi*: F, tibiotarsus, right distal end lacking inner condyle, USNM 496377 (anterior view); G, tibiotarsus, left distal end lacking inner condyle, USNM 496420 (anterior view); H, tarsometatarsus, right distal end lacking inner condyle, USNM 496419 (anterior view); I, same, posterior view. Scale is in 0.5 cm increments.

### Phoenicopteridae?

genus and species indeterminate

**Material:** Radii, right and left proximal ends, USNM 496388, 496389 (Fig. 4d). Collected by Tom Parks. Greatest proximal diameter, 6.7 mm.

Carpometacarpus, right proximal end, USNM 496385 (Fig. 4c). Collected by Chuck Ball. Proximal depth through alular metacarpal 14.1 mm, width of carpal trochlea 6.1 mm.

and depth, 3.7 X 4.8 mm.

**Discussion:** These are from a bird the size of the Old World Stone-curlew, *Burhinus oedipnemus*, to which the carpometacarpus bears some resemblance, although the ulna lacks the deep ligamental pit on the dorsal surface seen in the modern bird. They are here tentatively included as a smaller species of Graculavidae.

### Scolopaci

family, genus, and species indeterminate

**Material:** Humerus, right distal end lacking condyles, USNM 496374 (Fig. 3c). Collected by Tom Parks. Width just above ectepicondylar spur, 4.1 mm; width and depth of

shaft at approximate midpoint, 3.0 X 2.3 mm.

Tarsometatarsus, right distal end, USNM 496375 (Fig. 3d). Collected by Tom Parks. Distal width, 5.0 mm; width through outer and middle trochleae, 3.8 mm.

Pedal phalanx, probably phalanx 1 digit III, USNM 496376 (Fig. 3e). Collected by Mark Bennett. Length, 12.0 mm.

**Discussion:** These elements would all be compatible with a shorebird intermediate in size between the Old World and New World painted snipes (*Rostratula benghalensis* and *R. semicollaris*). The tarsometatarsus and humerus are clearly from some sort of limicoline charadriiform and the former compares better with the Rostratulidae than with the more derived families Scolopacidae and Charadriidae. The

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### Phoenicopteridae?

genus and species indeterminate

**Material:** Radii, right and left proximal ends, USNM 496388, 496389 (Fig. 4d). Collected by Tom Parks. Greatest proximal diameter, 6.7 mm.

Carpometacarpus, right proximal end, USNM 496385 (Fig. 4c). Collected by Chuck Ball. Proximal depth through alular metacarpal 14.1 mm, width of carpal trochlea 6.1 mm.

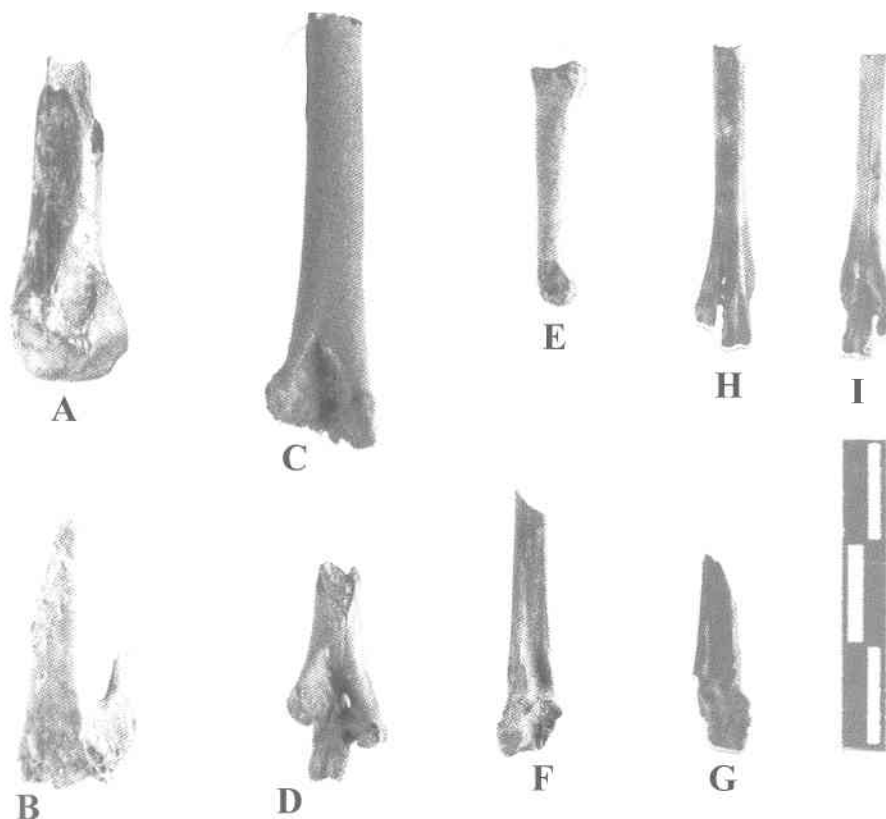


Figure 3. Various shorebird-like taxa. Graculavidae, genus and species indeterminate #2 : A, ulna, right distal end, USNM 496372 (internal view); B, carpometacarpus, right distal symphysis, USNM 496373 (internal view). Scolopaci, family, genus, and species indeterminate: C, humerus, right distal end lacking condyles, USNM 496374 (palmar view); D, tarsometatarsus, right distal end, USNM 496375 (posterior view); E, pedal phalanx, probably phalanx 1 digit III, USNM 496376 (lateral view). cf. *Coturnipes cooperi*: F, tibiotarsus, right distal end lacking inner condyle, USNM 496377 (anterior view); G, tibiotarsus, left distal end lacking inner condyle, USNM 496420 (anterior view); H, tarsometatarsus, right distal end lacking inner condyle, USNM 496419 (anterior view); I, same, posterior view. Scale is in 0.5 cm increments.

**Discussion:** The carpometacarpus is distinctive in the very long proximal symphysis, in which respect it is similar to modern flamingos (Phoenicopteridae), which have been shown to be derived from the Charadrii (Olson and Feduccia, 1980). The fossil carpometacarpus is from a bird slightly larger than in three females of the Lesser Flamingo (*Phoeniconaias minor*) but smaller than an unsexed, presumably male, individual of that species. The carpal trochlea is narrower in the fossil. The primitive flamingo *Juncitarsus* is known from early and middle Eocene deposits in Wyoming and Germany (Olson and Feduccia, 1980; Peters, 1987; Ericson, in press), although the two known species would probably have been somewhat smaller than the bird under consideration here.

The two radii listed above are most undiagnostic and are included here solely on size. Although they are from an individual smaller than that represented by the carpometacarpus, they could possibly be from the same species if the radii were from a female and the carpometacarpus from a male.

#### Order Incertae Sedis

cf. *Coturnipes cooperi* Harrison and Walker, 1977

**Material:** Tibiotarsus, right distal end lacking inner condyle, USNM 496377 (Fig. 3f). Collected by Mike Folmer. Depth of outer condyle, 3.2 mm.

Tibiotarsus, left distal end lacking inner condyle, USNM 496420 (Fig. 3g). Collected by Gary Grimsley. Width through outer and middle trochleae, 3.0 mm, depth of middle trochlea 2.0 mm.

Tarsometatarsus, right distal end lacking inner condyle, USNM 496419 (Fig. 3h,i). Collected by Mike Folmer. Depth of outer condyle, 3.2 mm.

**Discussion:** *Coturnipes cooperi* was described by Harrison and Walker (1977) as a new genus and species of small quail-like bird (Phasianidae) based on the distal end of a very small tarsometatarsus from the London Clay. I examined an associated skeleton from the London Clay in the collection of Michael Daniels, the tarsometatarsus of which I compared with the holotype of *Coturnipes cooperi*. I would consider these two specimens to be referable to the same species. The distal end of the tarsometatarsus is rather like that in the Phasianidae, but is also as similar to some of the Charadriiformes, with which the very long slender tibiotarsi and tarsometatarsi of the associated specimen are in better accord. Much of the remainder of the skeleton, however, is very suggestive of that in the Falconidae, which would be about as strange and inexplicable a mosaic as might be imagined. The phylogenetic significance of this weird bird remains to be investigated.

The Fisher/Sullivan Site tarsometatarsus is similar in size and morphology to the holotype of *Coturnipes cooperi*

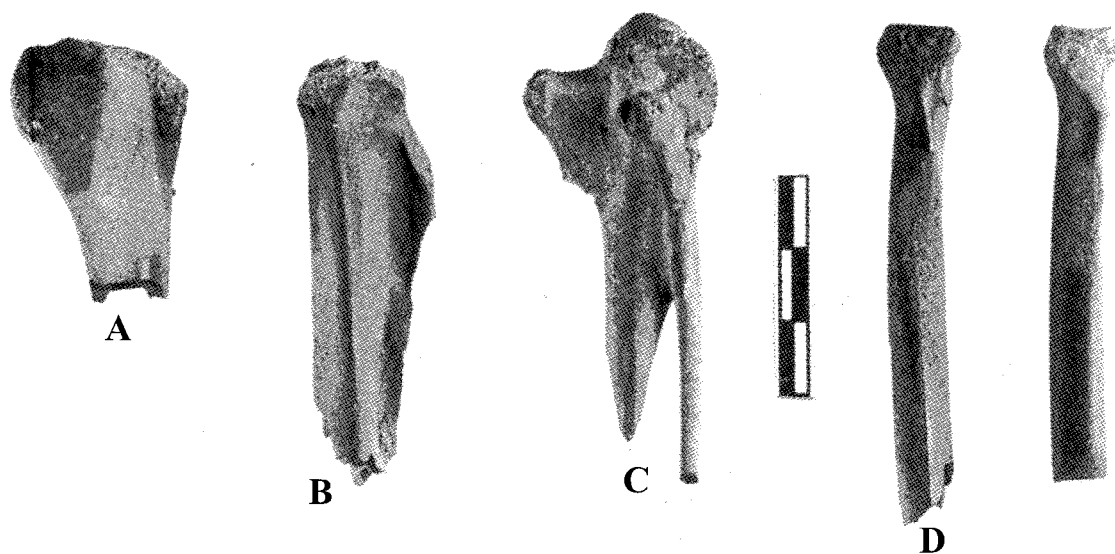


Figure 4. Crane-sized and flamingo-sized birds. Indeterminate crane-sized species: A, radius, left distal end with associated portion of shaft (not shown), USNM 496386 (exterior view); B, major alar digit, phalanx 1, USNM 496387 (external view). Phoenicopteridae?, genus and species indeterminate: C, carpometacarpus, right proximal end, USNM 496385 (internal view); D, radii, right and left proximal ends, USNM 496388, 496389. Scale is in 0.5 cm increments.

**Discussion:** The carpometacarpus is distinctive in the very long proximal symphysis, in which respect it is similar to modern flamingos (Phoenicopteridae), which have been shown to be derived from the Charadrii (Olson and Feduccia, 1980). The fossil carpometacarpus is from a bird slightly larger than in three females of the Lesser Flamingo (*Phoeniconaias minor*) but smaller than an unsexed, presumably male, individual of that species. The carpal trochlea is narrower in the fossil. The primitive flamingo *Juncitarsus* is known from early and middle Eocene deposits in Wyoming and Germany (Olson and Feduccia, 1980; Peters, 1987; Ericson, in press), although the two known species would probably have been somewhat smaller than the bird under consideration here.

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**Material:** Tibiotarsus, right distal end lacking inner condyle, USNM 496377 (Fig. 3f). Collected by Mike Folmer. Depth of outer condyle, 3.2 mm.

Tibiotarsus, left distal end lacking inner condyle, USNM 496420 (Fig. 3g). Collected by Gary Grimsley. Width through outer and middle trochleae, 3.0 mm, depth of middle trochlea 2.0 mm.

Tarsometatarsus, right distal end lacking inner condyle, USNM 496419 (Fig. 3h,i). Collected by Mike Folmer. Depth of outer condyle, 3.2 mm.

**Discussion:** *Coturnipes cooperi* was described by Harrison and Walker (1977) as a new genus and species of small quail-like bird (Phasianidae) based on the distal end of a very small tarsometatarsus from the London Clay. I examined an associated skeleton from the London Clay in the collection of Michael Daniels, the tarsometatarsus of which I compared with the holotype of *Coturnipes cooperi*. I would consider these two specimens to be referable to the same species. The distal end of the tarsometatarsus is rather like that in the Phasianidae, but is also as similar to some of the Charadriiformes, with which the very long slender tibiotarsi and tarsometatarsi of the associated specimen are in better accord. Much of the remainder of the skeleton, however, is very suggestive of that in the Falconidae, which would be about as strange and inexplicable a mosaic as might be imagined. The phylogenetic significance of this weird bird remains to be investigated.

The Fisher/Sullivan Site tarsometatarsus is similar in size and morphology to the holotype of *Coturnipes cooperi*

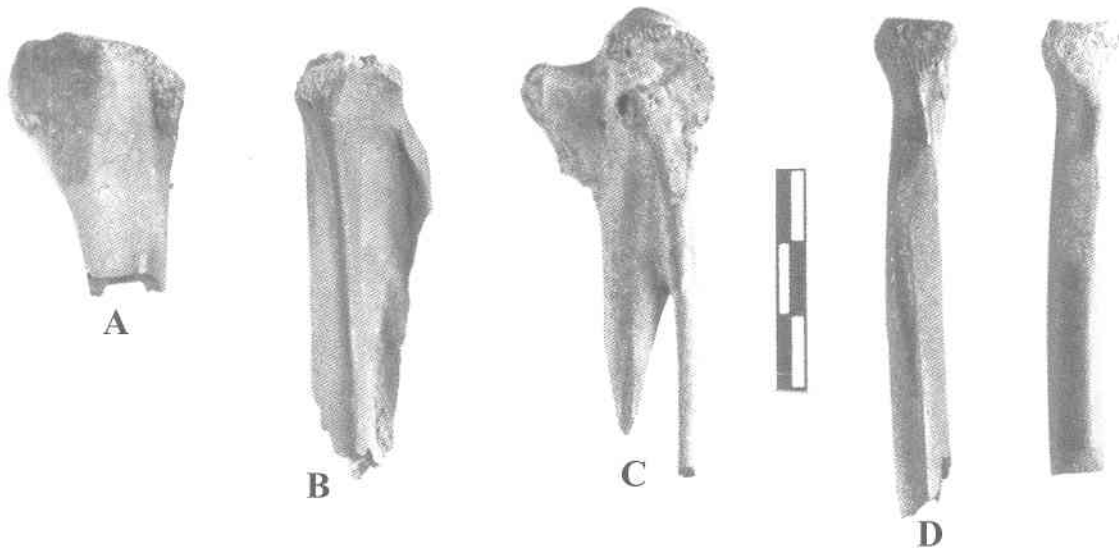


Figure 4. Crane-sized and flamingo-sized birds. Indeterminate crane-sized species: A, radius, left distal end with associated portion of shaft (not shown), USNM 496386 (exterior view); B, major alar digit, phalanx 1, USNM 496387 (external view). Phoenicopteridae?, genus and species indeterminate: C, carpometacarpus, right proximal end, USNM 496385 (internal view); D, radii, right and left proximal ends, USNM 496388, 496389. Scale is in 0.5 cm increments.

as described and illustrated by Harrison and Walker (1977). The two tibiotarsi referred here are very similar to each other and appear to be of a size and slenderness that would be compatible with the tarsometatarsus. They have a deep tendinal groove on the anterior face; a well-developed, wide, supratendinal bridge; and a long, triangular external ligamental prominence, in which respects they bear close resemblance to limicoline Charadriiformes, as does the tarsometatarsus. Referral of any of these specimens to *Coturnipes* must be considered tentative pending direct comparisons with the London Clay material.

**Caprimulgiformes**  
**Steatornithidae?**

genus and species indeterminate

**Material:** Humerus, left proximal end, USNM 496378 (Fig. 5a-c). Collected by Ron Keil. Proximal width, 15.7 mm; depth of external tuberosity, 4.6 mm.

Humerus, left distal end, USNM 496379 (Fig. 5d-f). Collected by Mike Folmer. Distal width, 13.1 mm; depth through radial condyle, 7.3 mm; length of radial condyle, 7.3 mm.

Tarsometatarsus, right outer trochlea, USNM 496418 (not figured). Collected by Mike Folmer. Depth of trochlea, 3.3 mm.

**Discussion:** The size, exquisite preservation, morphology, and the fact that both of the humeral fragments (Fig. 5a-f) are from the same side of the body make it virtually certain that they are ends of one and the same bone. They come from a bird intermediate in size between the Long-tailed Potoo, *Nyctibeus aethereus*, and the smaller Common Potoo, *N. griseus*.

The closest overall similarity of these fragments is to the Nyctibiidae, but it must be kept in mind that the humerus in the living Oilbird, *Steatornis caripensis*, is highly specialized and does not resemble that in the only known Eocene member of the Steatornithidae, *Prefica nivea* (Olson, 1987). Most details of the humerus cannot be made out in the holotype of *Prefica nivea*, although this was a considerably smaller species than the one under consideration here (Olson, 1987).

The proximal end of the humerus closely resembles that of *Nyctibius* in the long, flat head; wide capital groove; and high, pointed internal tuberosity overhanging a small pneumatic opening in the tricipital fossa. It differs from *Nyctibius* in the more prominent median ridge on the anconal surface of the shaft and particularly in the less developed bicipital crest, so that the margin tapers directly from the internal tuberosity to the shaft rather than being rounded.

The distal end is also rather like that in *Nyctibius*, but is distinctive in being very flattened, with very little curvature of the shaft as viewed internally or externally. The distal

end is not as broadly expanded, particularly in the entepicondylar region, as in *Nyctibius*, and the brachial depression differs considerably in being less extensive but much deeper.

The shape of the bicipital crest and the brachial depression can be viewed as similar to, or approaching, the condition in *Steatornis*. Thus it seems possible that this bird may have been a larger relative of *Prefica*, without the more specialized modifications of the humerus seen in *Steatornis*.

At first sight the metatarsal trochlea would appear to defy identification but it preserves enough of the shaft and the impression of the extensor groove as to be highly diagnostic. This trochlea would have been highly flared laterally and the distal foramen clearly exited between the outer and middle trochleae and not on the plantar surface of the shaft, both of which features are found in the Nyctibiidae and Steatornithidae. The articular surface for the proximal phalanx is not highly modified as in modern Nyctibiidae. On size, the specimen appears to be compatible with the same species as represented by the humeral fragments.

**Caprimulgidae?**

genus and species indeterminate #1

**Material:** Humerus, left proximal two-thirds, USNM 496380 (Fig. 6a,b). Collected by Tom Parks. Proximal width, 9.0 mm; width and depth of shaft at approximate midpoint, 2.8 X 2.5 mm.

Radius, right distal half, USNM 496381 (Fig. 6c,d). Collected by Tom Parks. Greatest distal diameter, 3.1 mm.

Tarsometatarsus, left distal end lacking inner trochlea and with remaining trochleae quite worn, USNM 496382 (Fig. 6e,f). Collected by Dick Grier, Jr. Width through outer and middle trochleae, 3.4 mm.

**Discussion:** These three elements appear to be from a nightjar-like bird about the size of a Parouque, *Nyctidromus albigollis*. The humerus and radius were obtained by the same collector, were evidently found about the same time, and have very similar preservation. The radius shows some differences from that of *Nyctidromus albigollis* but is almost exactly the same size and would be much larger than in a shorebird of otherwise comparable size, so its association with the same species as the humerus seems reasonable.

The humerus (Figure 6a,b) is very similar in size and overall configuration of the proximal end to that of *Nyctidromus albigollis* (Caprimulgidae). It differs in the more slender shaft, longer and more distally situated pectoral crest, more prominent median ridge, and much less prominent area below the internal tuberosity for the attachment of the scapulohumeralis posterior muscle.

The tarsometatarsus (Figure 6e,f), with its rather broad, flattened end and widely splayed trochleae, is highly

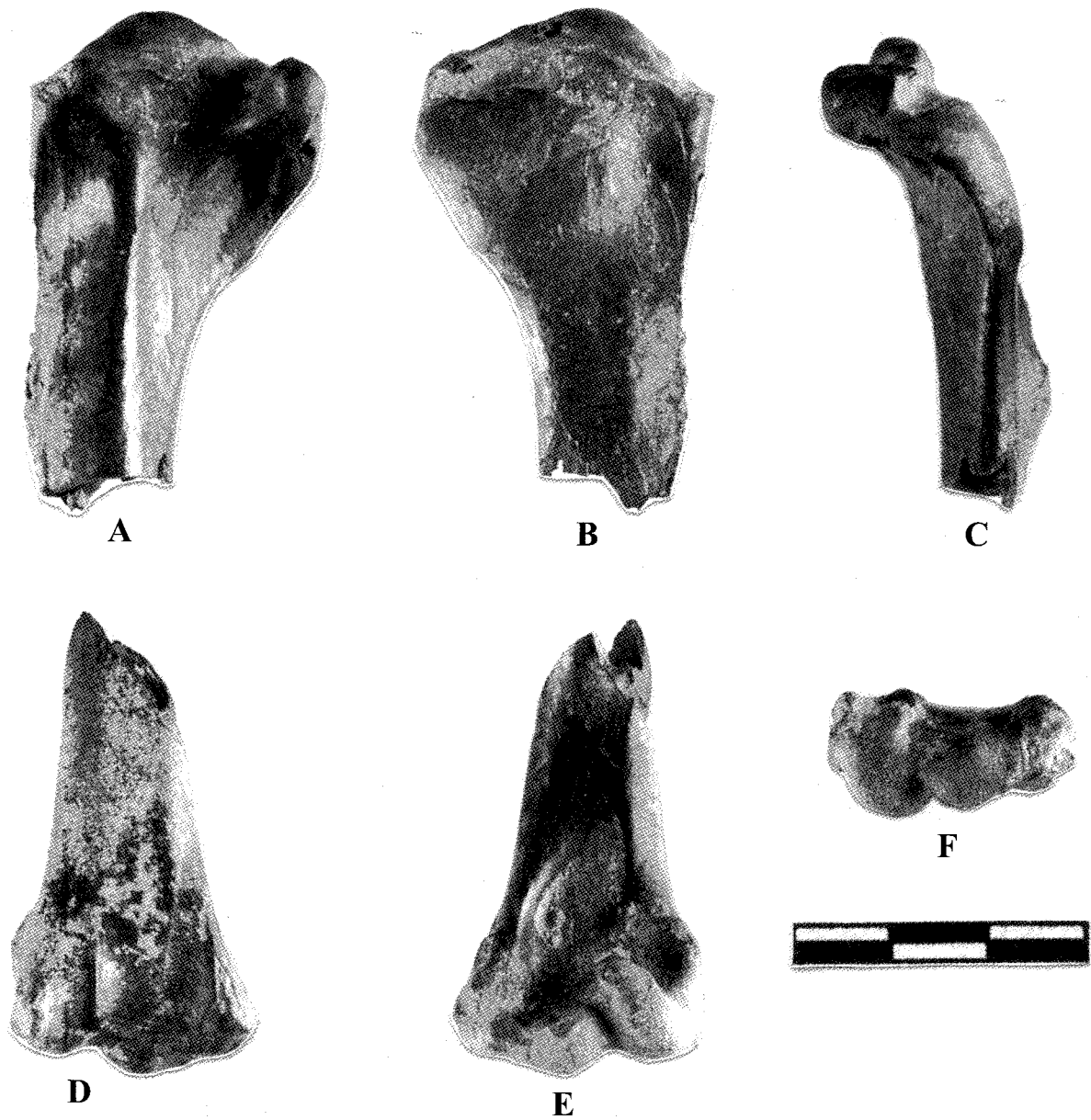


Figure 5. *Steatornithidae*?, genus and species indeterminate: A-C, humerus, left proximal end, USNM 496378 (A, anconal; B, palmar; and C, internal view); D-F, humerus, left distal end, USNM 496379 (D, anconal; E, palmar; and F, distal view). Scale is in 0.5 cm increments.

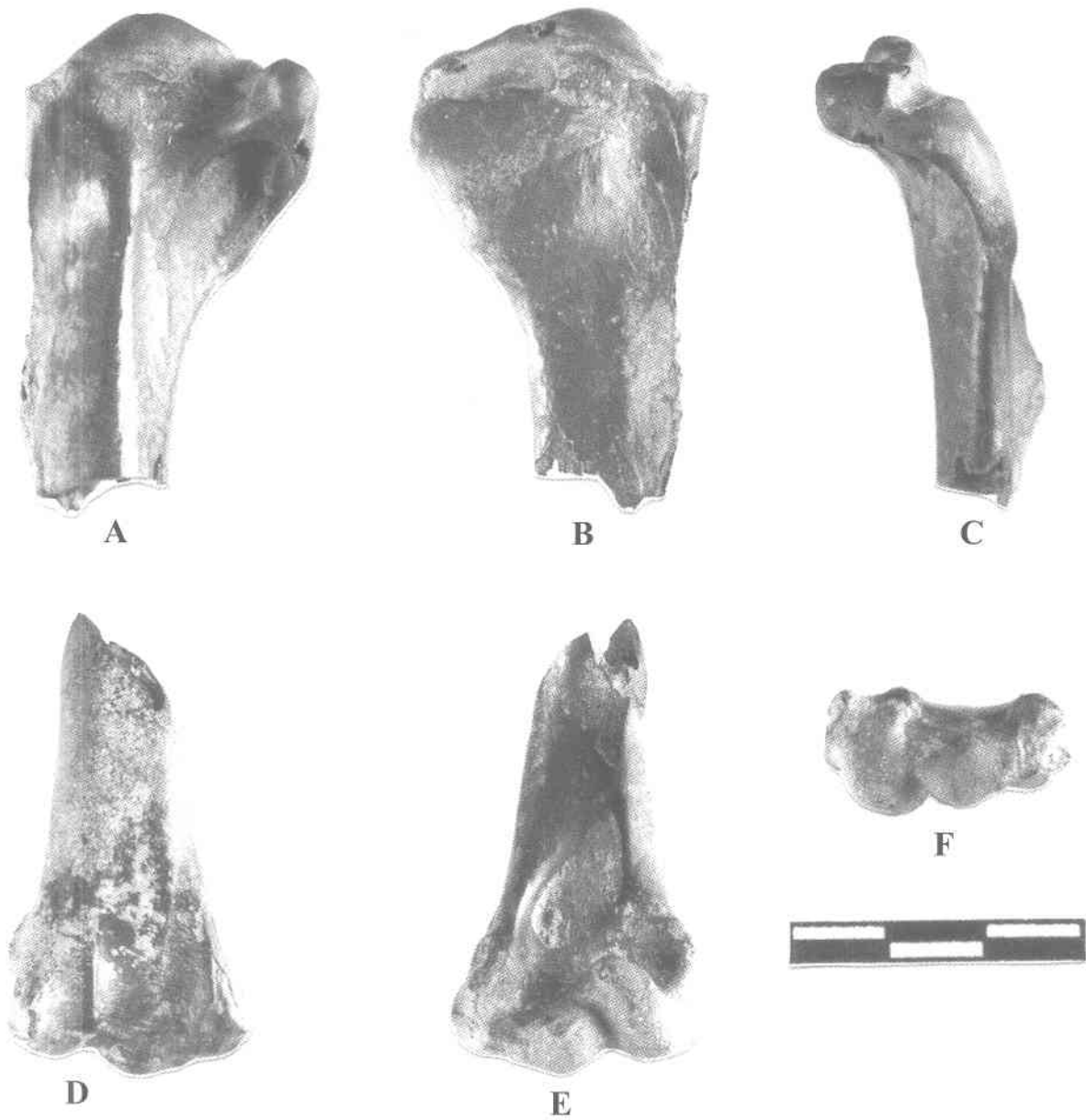


Figure 5. *Steatornithidae?*, genus and species indeterminate: A-C, humerus, left proximal end, USNM 496378 (A, anconal; B, palmar; and C, internal view); D-F, humerus, left distal end, USNM 496379 (D, anconal; E, palmar; and F, distal view). Scale is in 0.5 cm increments.

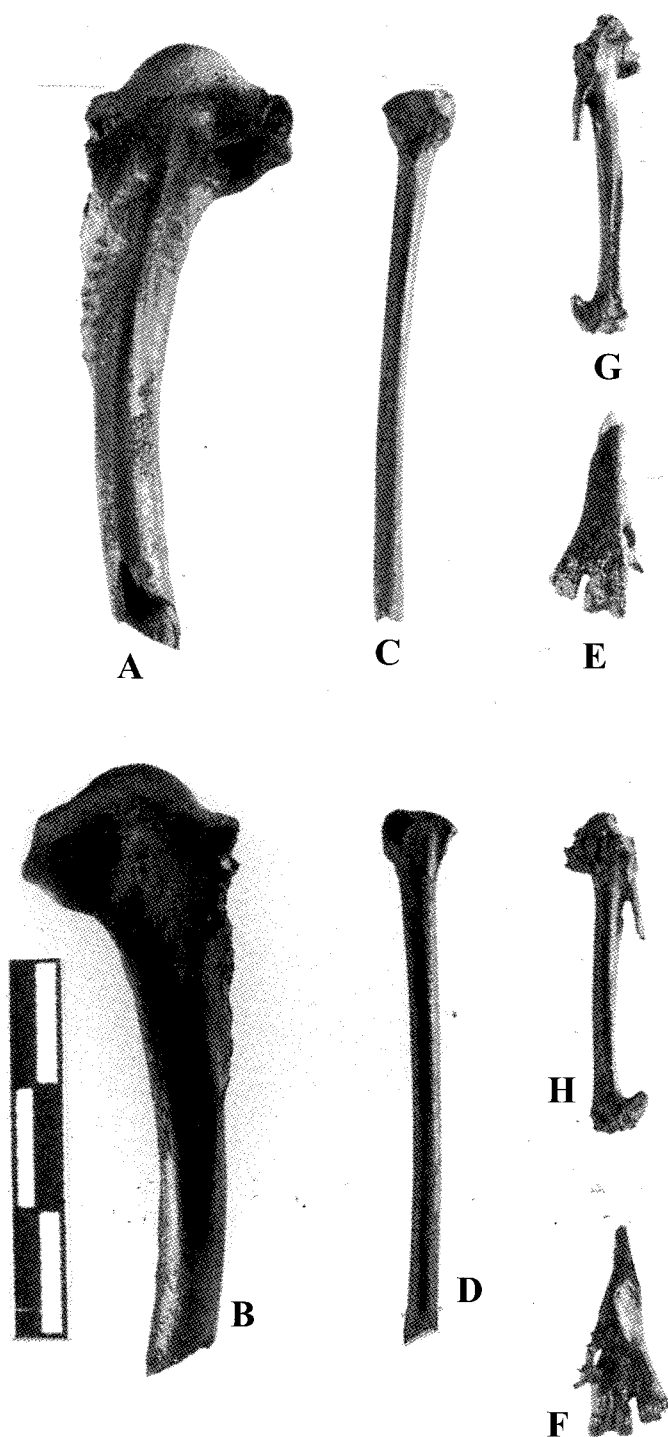


Figure 6. Two species similar to modern Caprimulgidae. Caprimulgidae?, genus and species indeterminate #1: A-B, humerus, left proximal two-thirds, USNM 496380 (A, anconal; B, palmar view); C-D, radius, right distal half, USNM 496381 (C, internal; D, external view); E-F, tarsometatarsus, left distal end, USNM 496382 (E, anterior; F, posterior view). Caprimulgidae?, genus and species indeterminate #2: G-H, carpometacarpus, right USNM 496383 (G, external; H, internal view). Scale is in 0.5 cm increments.

reminiscent of that in the Caprimulgidae, but differs from *Nyctidromus* in the much larger distal foramen, and in the size and positioning of the scar for the hallux. In the fossil, this scar is very well developed, being long and deep, whereas in the Caprimulgidae the scar, although large, is flatter and has a medially projecting lip that extends beyond the outline of the shaft, unlike the fossil. I regard it as highly likely that this specimen belongs to the same species as the humerus.

genus and species indeterminate #2

**Material:** Carpometacarpus, right lacking most of minor metacarpal, USNM 496383 (Fig. 6g,h). Collected by Mike Folmer. Length, 13.2 mm.

**Discussion:** This is from a quite small bird, the carpometacarpus being only slightly longer than that of a House Sparrow, *Passer domesticus*, though the bird was doubtless of very different proportions. Compared with *Nyctidromus albicollis*, the fossil is almost identical except for smaller size and the more rounded external margin of the trochlea, which is thus not as sharply set off from the alular metacarpal. There is even a small protuberance on the trailing edge of the proximal end of the major metacarpal--probably an incipient intermetacarpal tubercle--just as in the Caprimulgidae.

The resemblances are so great that there can be no doubt that this bone is correctly referred to the Caprimulgiformes. Were it not for the fact that it is early Eocene in age and that there are no species in this size range among the modern Caprimulgidae, I would have little hesitation in referring it with certainty to that family. The species may have occupied a different niche from that of modern nightjars, although the bone shows no indication of any of the adaptations of the wing found in swift-like birds (Apodiformes).

#### Order Apodiformes

##### Aegialornithidae

genus and species indeterminate

**Material:** Tarsometatarsus, right complete, USNM 496384 (Fig. 7a,b). Collected by Chuck Ball. Length 11.8 mm, proximal width 3.8 mm, distal width 3.8 mm.

**Discussion:** The extinct fossil family Aegialornithidae is generally thought to be related to swifts (Apodidae) but has also been placed in the

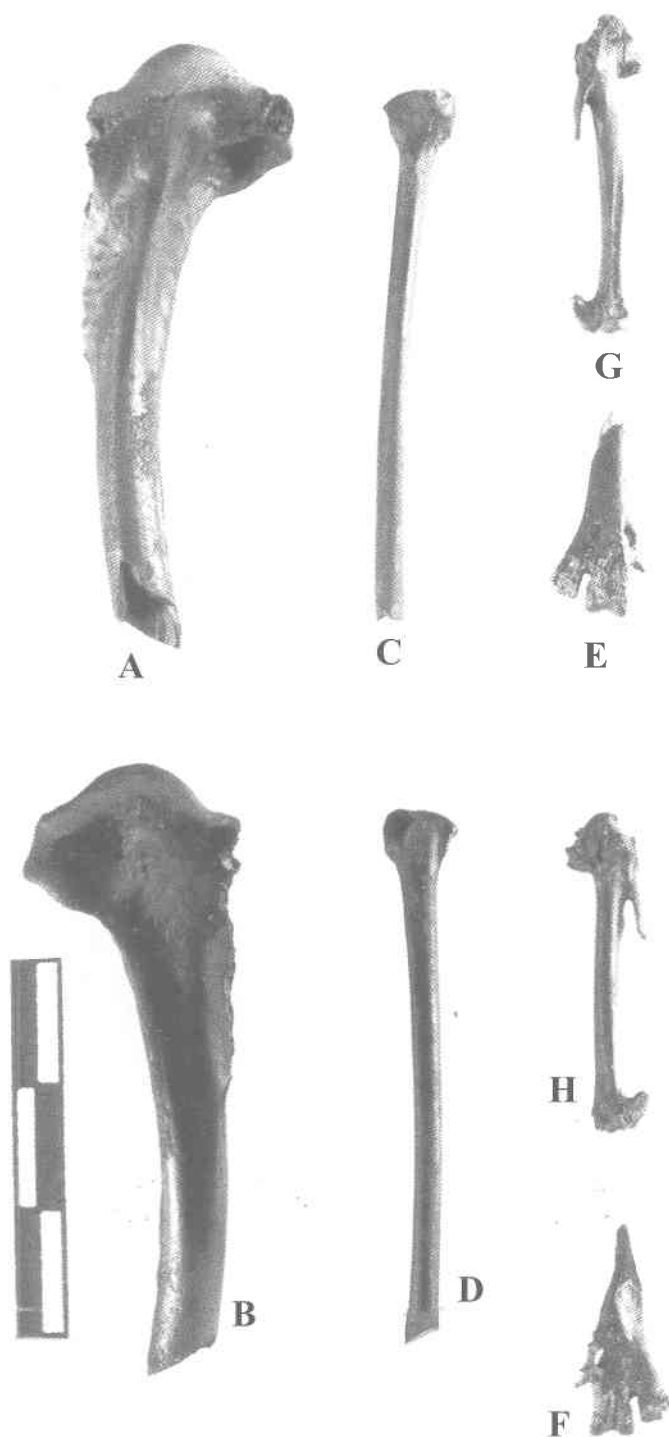


Figure 6. Two species similar to modern Caprimulgidae. Caprimulgidae?, genus and species indeterminate #1: A-B, humerus, left proximal two-thirds, USNM 496380 (A, anconal; B, palmar view); C-D, radius, right distal half, USNM 496381 (C, internal; D, external view); E-F, tarsometatarsus, left distal end, USNM 496382 (E, anterior; F, posterior view). Caprimulgidae?, genus and species indeterminate #2: G-H, carpometacarpus, right USNM 496383 (G, external; H, internal view). Scale is in 0.5 cm increments.

reminiscent of that in the Caprimulgidae, but differs from *Nyctidromus* in the much larger distal foramen, and in the size and positioning of the scar for the hallux. In the fossil, this scar is very well developed, being long and deep, whereas in the Caprimulgidae the scar, although large, is flatter and has a medially projecting lip that extends beyond the outline of the shaft, unlike the fossil. I regard it as highly likely that this specimen belongs to the same species as the humerus.

genus and species indeterminate #2

**Material:** Carpometacarpus, right lacking most of minor metacarpal, USNM 496383 (Fig. 6g,h). Collected by Mike Folmer. Length, 13.2 mm.

**Discussion:** This is from a quite small bird, the carpometacarpus being only slightly longer than that of a House Sparrow, *Passer domesticus*, though the bird was doubtless of very different proportions. Compared with *Nyctidromus albicollis*, the fossil is almost identical except for smaller size and the more rounded external margin of the trochlea, which is thus not as sharply set off from the alular metacarpal. There is even a small protuberance on the trailing edge of the proximal end of the major metacarpal--probably an incipient intermetacarpal tubercle--just as in the Caprimulgidae.

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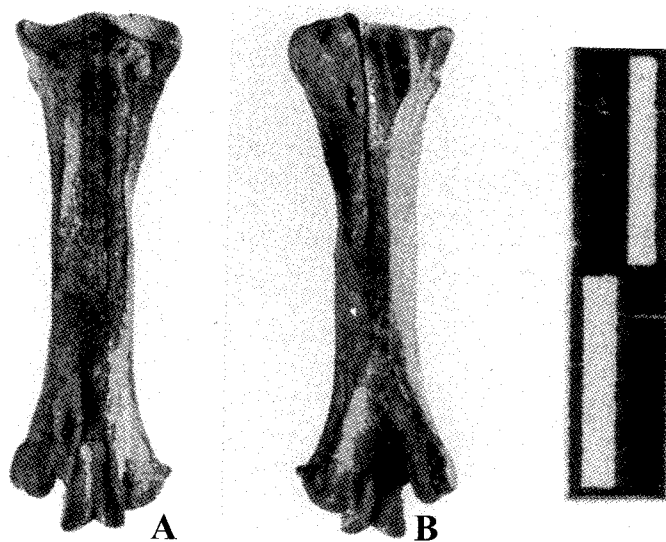


Figure 7. Aegialornithidae, genus and species indeterminate: tarsometatarsus, right complete, USNM 496384 (A, anterior; B, posterior view). Scale is in 0.5 cm increments.

Caprimulgiformes (Collins, 1976). The genus *Aegialornis* is known from four species from the late Eocene and Oligocene of France, the most abundant element of which is the humerus. A much smaller species, also based on humeri, was described from the London Clay as *Primapus lacki* (Harrison and Walker, 1975). In describing another small species from the middle Eocene of Germany, Peters (1985) considered that the differences between *Primapus* and *Aegialornis* were not as great as between the species of the latter and synonymized the two genera, naming his new bird *Aegialornis szarskii*. Mourer-Chauviré (1988) resurrected *Primapus* for *P. lacki* and *P. szarskii*.

A beautifully preserved tarsometatarsus from the Fisher/Sullivan Site (Fig. 7a,b) is similar to that of *Aegialornis gallicus* illustrated by Mourer-Chauviré (1988: 375) but is much stouter. The tarsometatarsus in *A. gallicus* ranges from 13.3 to 14.7 mm in length (Mourer-Chauviré, 1988: 377), so the present fossil could possibly fall within the size range of the smaller species *A. wetmorei* or *A. broweri* (Collins, 1976), for which the tarsometatarsus is apparently unknown. The tarsometatarsus of *Primapus lacki* has not been described and Peters gives no measurements for that of *P. szarskii*, although from his photographs it is seen that the tarsometatarsus is about equal in length to phalanx 1 of the major alar digit, the length of which is given as 6 mm. Thus the two known species of *Primapus* are much too small for the bird considered here. If correctly referred to the Aegialornithidae, the present specimen would constitute the first record of the family outside of Europe.

#### Aves, indeterminate species (crane-sized)

**Material:** Radius, left distal end with associated portion of shaft, USNM 496386 (Fig. 4a). Collected by Chuck Ball. Greatest distal diameter, 12.5 mm.

Major alar digit, phalanx 1, proximal half lacking much of the trailing edge, USNM 496387 (Fig. 4b). Collected by Mike Folmer. Greatest proximal diameter, 9.8 mm.

**Discussion:** The radius is similar in size to that of a Sandhill Crane, *Grus canadensis*, and is also reasonably similar in morphology. The wing finger is of a size possibly compatible with the radius. Although the radius is at least roughly similar to that of cranes, the wing finger is quite different in having the external surface deeply excavated, whereas the internal surface is peculiar in being almost a synoptic series of avian skeletal elements at the Smithsonian does not include this element, so further comparisons were not attempted. Size, therefore, is the only reason for associating these two elements, which come from a species smaller than the pseudodontorn but larger than any other taxon yet recognized in the fauna.

#### Indeterminate avian pedal phalanges

**Material:** Two pedal phalanges collected by Mike Folmer, USNM 496390, 496391 (lengths, 6.4 and 9.3 mm). Two pedal phalanges collected by Chuck Ball, USNM 496421, 496422 (lengths, 12.2 and 11.2 mm).

**Discussion:** I have made no attempt to identify these four toe bones, all of which, however, appear to be too short or curved to be likely to be from terrestrial or wading birds and hence may have been from arboreal species. Some or all of the specimens may be referable to one or more of the species already noted in the fauna.

#### CONCLUSION

The avifauna from the Fisher/Sullivan Site is represented only by 33 bones or fragments thereof, yet these few remains appear to belong to a minimum of 11 different species, so that the faunule is extremely diverse given the very small sample size. Although coming from a marine deposit, only one of the 11 species (the pseudodontorn) was certainly pelagic, the rest being land birds. Some of these may have inhabited littoral environments, but at least the four species of Caprimulgiformes/Apodiformes would have been dependent upon purely inland ecosystems, probably forested. Although the Caprimulgidae proper are now widespread in temperate and tropical regions, all other families of the order are confined to tropical forests. A similar environment may thus be inferred for the Fisher/Sullivan Site deposits, particularly from the presence of the specimens tentatively referred to the Steatornithidae.

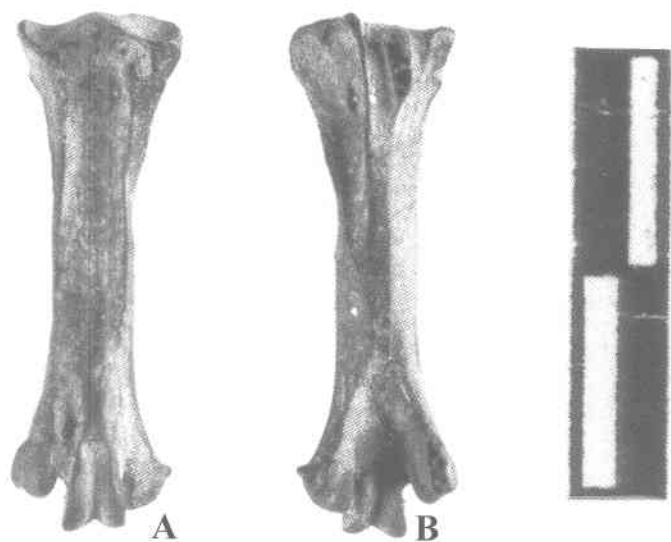


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There is some similarity to the early Eocene London Clay deposits at Walton-on-the-Naze, Essex, England. There the deposits, the exposures of which are relatively limited in area, are strictly offshore marine in nature, yet the fossil vertebrates are dominated by birds, particularly small arboreal species. One wonders if the parallels between the deposits at Walton-on-the-Naze and those at the Fisher/Sullivan Site, where a considerable diversity of land birds also occurred in a very small area, might be due to the effects of similar depositional conditions. In any case, the Fisher/Sullivan Site material provides us with a tantalizing first glimpse into the early Eocene avifauna of eastern North America. The deposits here would be well worth working for additional fossils. The birds from this site will assume even greater importance when they can be compared in detail with other specimens of similar age, particularly those from the London Clay. It is highly likely that correlations at the species level will be possible, because certain species of birds are already known to be shared between the London Clay and deposits of similar age in Wyoming.

#### ACKNOWLEDGMENTS

I am grateful to Robert Weems for coordinating the Fisher/Sullivan Site project and bringing this most interesting assemblage of fossil birds to my attention. He and I are heavily indebted to the collectors who worked so hard to process matrix from the site, without which we would still know nothing about the early Eocene birds of eastern North America. Those who collected fossil birds are: Chuck Ball, Mark Bennett, Richard Brezina, Mike Folmer, Dick Grier, Jr., Gary Grimsley, Ron Keil, and Tom Parks. Fred Grady cleaned some of the specimens and Mark Florence processed and cataloged them all expeditiously and checked the manuscript against the collection data. For the insights I have gained into the avifauna of the London Clay, I am indebted to Michael Daniels, who allowed access to his collections. I am especially grateful to Carl Hansen of the Smithsonian Photographic Services for providing photographs of such fine quality upon very short notice.

#### BIBLIOGRAPHY

- Andors, A. V., 1988, Giant groundbirds of North America (Aves: Diatrymidae). Ph. D. dissertation, Columbia University, New York (University Microfilms order no. 8815650).
- Collins, C. T., 1976, Two new species of *Aegialornis* from France, with comments on the ordinal affinities of the Aegialornithidae. *Smithsonian Contributions to Paleobiology*, v. 27, p. 121-127.
- Ericson, P., In press, New material of *Juncitarsus* (Phoenicopteriformes) with a guide for differentiating that genus from the Presbyornithidae (Anseriformes). *Smithsonian Contributions to Paleobiology*, v. 89.
- Gingerich, P. D., ed., 1980, Early Cenozoic paleontology and stratigraphy of the Bighorn Basin, Wyoming. *University of Michigan Papers on Paleontology*, no. 24, 146 p.
- Harrison, C. J. O., and C. A. Walker, 1975, A new swift from the Lower Eocene of Britain. *Ibis*, v. 117, p. 162-164.
- Harrison, C. J. O., and C. A. Walker, 1977, Birds of the British Lower Eocene. *Tertiary Research Special Paper*, no. 3, 52 p.
- Houde, P. W., 1988, Paleognathous birds from the early Tertiary of the Northern Hemisphere. *Publications of the Nuttall Ornithological Club*, v. 22, 148 p.
- Houde, P., and S. L. Olson, 1989, Small arboreal non-passerine birds from the early Tertiary of western North America. *Acta XIXth Congressus Internationalis Ornithologici*, v. 2 [for 1988], p. 2030-2036.
- Houde, P., and S. L. Olson, 1992, A radiation of coly-like birds from the early Eocene of North America (Aves: Sandcoleiformes new order). *Science Series, Natural History Museum of Los Angeles County*, v. 36, p. 137-160.
- Mourer-Chauviré, C., 1988, Les Aegialornithidae (Aves: Apodiformes) des Phosphorites du Quercy. Comparaison avec la forme de Messel. *Courier Forschungsinstitut Senckenberg*, v. 107, p. 369-381.
- Olson, S. L., 1985, The fossil record of birds, in D. S. Farner, J. R. King, and K. C. Parkes, eds., *Avian Biology*, v. 8, p. 79-238. Academic Press: New York and London.
- Olson, S. L., 1987, An early Eocene oilbird from the Green River Formation of Wyoming (Caprimulgiformes: Steatornithidae). *Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon*, v. 99, p. 57-69.
- Olson, S. L., 1994, A giant *Presbyornis* (Aves: Anseriformes) and other birds from the Paleocene Aquia Formation of Maryland and Virginia. *Proceedings of the Biological Society of Washington*, v. 107, no. 3, p. 429-435.
- Olson, S. L., In press, The anseriform relationships of *Anatalavis* Olson and Parris (Anseranatidae), with a new species from the Lower Eocene London Clay. *Smithsonian Contributions to Paleobiology*, v. 89.
- Olson, S. L. and A. Feduccia, 1980, Relationships and evolution of flamingos (Aves: Phoenicopteridae). *Smithsonian Contributions to Zoology*, v. 316, 73 p.
- Olson, S. L. and D. C. Parris, 1987, The Cretaceous birds of New Jersey. *Smithsonian Contributions to Paleobiology*, v. 63, 22 p.
- Peters, D. S., 1985, Ein neuer Segler aus der Grube Messel und seine Bedeutung für den Status der Aegialornithidae (Aves: Apodiformes). *Senckenbergiana Lethaea*, v. 66, p. 143-164.
- Peters, D. S., 1987, *Juncitarsus merkeli* n. sp. stützt die Ableitung der Flamingos von Regenpfeifervögeln (Aves: Charadriiformes: Phoenicopteridae). *Courier Forschungsinstitut Senckenberg*, v. 97, p. 141-155.

## PART 7. FOSSIL MAMMALS FROM THE EARLY EOCENE FISHER/SULLIVAN SITE

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### ABSTRACT

Seven mammalian specimens have been found at the Fisher/Sullivan site, constituting the first early Eocene mammals from the Atlantic coast of North America. One is a cervical vertebra, possibly from an ischyromyid rodent. Five others are isolated teeth, which are most comparable to the tillodont *Esthonyx*, the tapiromorph perissodactyl *Homogalax*, the pantolestid *Palaeosinopa*, the condylarth *Hyopsodus*, and the miacid carnivore *Oodectes*. A lower jaw fragment with three teeth represents what is possibly a new genus and species of nyctitheriid insectivoran. These taxa are typical members of early Eocene (Wasatchian Land-Mammal Age) vertebrate assemblages from the intermontane basins of western North America.

### INTRODUCTION

Early Tertiary land mammals are extremely rare from the Atlantic and Gulf coastal region of North America. Only 10 known sites, scattered from New Jersey to southern Texas, have produced Paleocene or Eocene terrestrial mammals; five of these sites have yielded but a single specimen. The nearshore marine Shark River Formation (middle Eocene) of Monmouth County, New Jersey was the source, over a century ago, of the first early Tertiary mammal discovered east of the Rocky Mountains (Leidy, 1868; Gazin, 1953). The specimen, an isolated tooth of a trogosine tillodont, is still the only known land mammal from that formation. A late Paleocene site in Berkeley County, South Carolina, produced a few mammal teeth, one identified as belonging to the taeniodont *Ectoganus*, a second as belonging to the condylarth *Phenacodus*, and a third from an enigmatic new placental called *Mingotherium*; two others were indeterminate (Schoch, 1985, 1998). Farther south, unidentified land mammals have been reported from a late Eocene locality in Georgia (Schiebout, 1979).

Paleocene or Eocene mammals are known from several sites on the Gulf Coast. The oldest is a partial skull of the Middle Paleocene condylarth *Anisonchus*, serendipitously discovered in a well core in Louisiana (Simpson, 1932). Middle Eocene sites in Mississippi and Alabama have yielded single specimens of a titanothere (Gazin and Sullivan, 1942) and a miacid carnivore (Schiebout, 1979), respectively. An early Eocene primate was recently reported from the Bashi Formation of Mississippi (Beard and Tabrum, 1991), and subsequent work in the underlying estuarine Tusahoma Formation at this site has resulted in one of only two diverse early Tertiary faunas from eastern North America—the Red Hot local fauna, with 25 species of land mammals (Beard et al., 1995). The only other sizable Eocene terrestrial mammal

fauna (>30 species) from this region is the Middle Eocene (Uintan) Casa Blanca local fauna from the Laredo Formation of Texas (Westgate, 1988, 1990).

Clearly, what little knowledge we have of early Tertiary mammals in eastern North America is limited largely to the Gulf coastal region. In view of this paucity of information, the discovery of mammal remains from early Eocene deposits near Fredericksburg, Virginia, is an important addition to our knowledge.

### DESCRIPTIVE PALEONTOLOGY

To date, only seven very incomplete mammalian specimens have been found at the Fisher/Sullivan Site (Potapaco Member of the Nanjemoy Formation), but they are significant as the first early Tertiary mammal remains known from Virginia and the first early Eocene (Wasatchian) mammals known from anywhere along the Atlantic coast of North America. In North America, Wasatchian mammals long have been known almost exclusively from the Rocky Mountain region (Savage and Russell, 1983). For this reason, comparisons with the specimens described here are made mostly with specimens from that area. Institutional acronyms used in the descriptions below are: UM = University of Michigan Museum of Paleontology, Ann Arbor; USGS = U.S. Geological Survey, Denver, collection now at USNM; USNM = Department of Paleobiology, U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C.

One of the seven Fisher/Sullivan mammal remains is a cervical (neck) vertebra (USNM 494878, Fig. 1) collected by Tom Parks. It is identified as the seventh cervical vertebra, or C7, on the basis of the very large vertebral foramen (for passage of the spinal cord) and the absence of transverse foramina (which transmit the vertebral arteries through cervicals 1–6 in most mammals). The centrum is elliptical, half again as wide transversely as it is deep dorsoventrally, and has a distinct median ventral keel. On either side of the keel is a small nutrient foramen. Larger vascular foramina are situated on the dorsal side of the centrum. The centrum is skewed so that the dorsal edge of both ends is anterior (cranial) to the ventral edge. The laminae are robust and contain a pair of small nutrient foramina. Unlike C7 in many mammals, the spinous process is relatively small. In most of these features, as well as size, the vertebra is similar to C7 of the living squirrel, *Sciurus*

*niger*. Because it is somewhat porous and light, the Eocene age of this specimen at first appeared questionable; however, like other vertebrate fossils from the site, it is very dark and appears to be permineralized. Grains of pyrite or marcasite can be seen in foramina and along broken edges filling some of the spaces in the bone. Thus the vertebra does not appear to be a contaminant, and its resemblance to C7 of modern squirrels suggests that it may belong to an ischyromyid rodent. Ischyromyids were primitive rodents, generally similar in size and postcranial anatomy to sciurids, and they are well known from Eocene beds of western North America. Diagnostic traits of small Eocene mammal vertebrae are poorly known, however, so definitive identification is not yet possible.

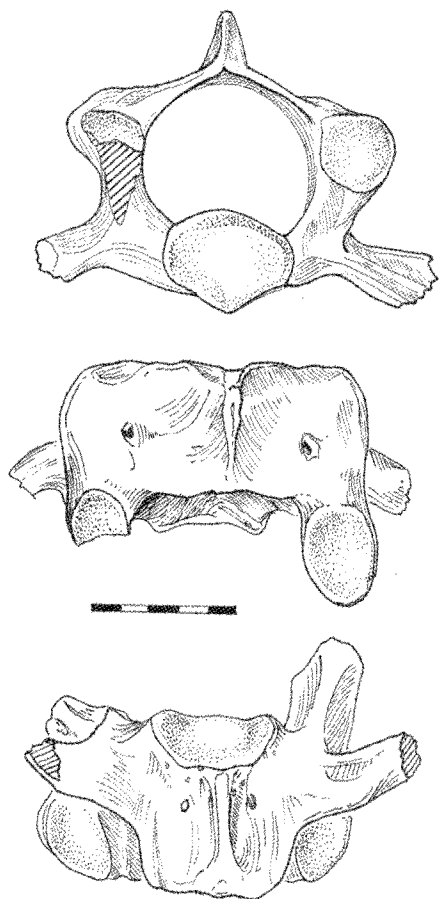


Figure 1. Cervical vertebra of a small mammal, possibly an ischyromyid rodent (USNM 494878), in anterior, dorsal, and ventral views. Scale bar is 5 mm.

The other specimens are teeth or include teeth, which are unequivocally fossilized and evidently belong to Wasatchian terrestrial mammals. The first mammal tooth found at the site, apparently the right upper canine of a moderate-sized animal (USNM 494879, Fig. 2), was found by Michael A. Folmer. The crown measures 6.2 mm long, 3.9 mm wide, and 7.6 mm in buccal crown height. Isolated canine teeth may be difficult or impossible to identify with confidence, but the tooth in question is distinctive in being low crowned

(only slightly taller than long) and laterally compressed, and in having faintly wrinkled enamel. The crest anterior to the apex is shorter than the posterior crest; when viewed in profile the two crests meet at a wide angle, almost 90°. A flattened wear facet present on the posterointernal surface of the crown was presumably caused by contact with the anterior lower premolar.

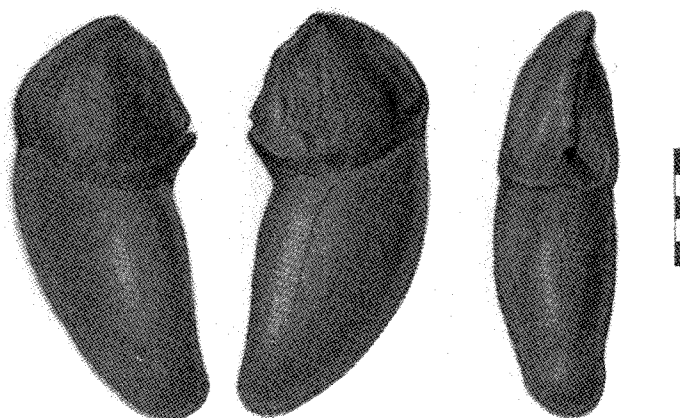


Figure 2. Right upper canine of the tillodont *Esthonyx* (?) (USNM 494879), in buccal, lingual, and distal views. Scale bar is 5 mm.

In size and structural details including the textured enamel, this tooth closely approximates the few known upper canines (more specifically, the deciduous canine) of the tillodont *Esthonyx* from the Wasatchian of western North America (e.g., UM 96053, USGS 10258, USNM 495050, all from the Willwood Formation of the Bighorn Basin, Wyoming). *Esthonyx* upper canines differ from the Fisher/Sullivan tooth, however, in being more robust labiolingually and in having a prominent vertical ridge near the middle of the lingual side of the tooth. USGS 10258 contains a deciduous (=“milk”) canine, which is not as thick labiolingually and has a much weaker vertical ridge. It is quite similar, though not identical, to the Fisher/Sullivan tooth. Almost identical, however, is an isolated right upper canine (USNM 495049) recently recovered from the Willwood Formation and believed to represent *Esthonyx*. Size and morphology substantially restrict the taxa the Fisher/Sullivan tooth could represent, and of known Wasatchian mammals it resembles *Esthonyx* more closely than any other.

*Esthonyx* has not been previously reported from east of the Rockies in North America, but closely related tillodont genera are known from the early Eocene of western Europe (Baudry, 1992). Moreover, as noted above, a closely related trogosine tillodont from the middle Eocene of New Jersey is one of the few Eocene mammals known from eastern North America. Tillodonts have no living relatives and are still among the most enigmatic Early Tertiary mammals. Heavy tooth wear and enlarged incisors, supplemented by scattered skeletal remains, suggest that their diet consisted of roots,

*niger*. Because it is somewhat porous and light, the Eocene age of this specimen at first appeared questionable; however, like other vertebrate fossils from the site, it is very dark and appears to be permineralized. Grains of pyrite or marcasite can be seen in foramina and along broken edges filling some of the spaces in the bone. Thus the vertebra does not appear to be a contaminant, and its resemblance to C7 of modern squirrels suggests that it may belong to an ischyromyid rodent. Ischyromyids were primitive rodents, generally similar in size and postcranial anatomy to sciurids, and they are well known from Eocene beds of western North America. Diagnostic traits of small Eocene mammal vertebrae are poorly known, however, so definitive identification is not yet possible.

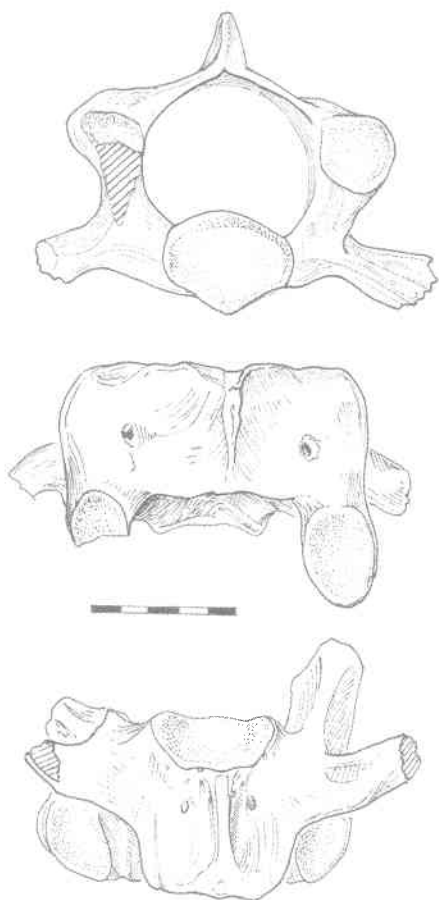


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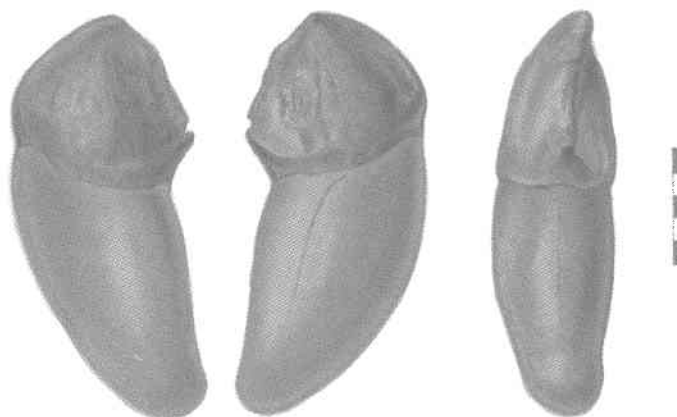


Figure 2. Right upper canine of the tillodont *Esthonyx* (?) (USNM 494879), in buccal, lingual, and distal views. Scale bar is 5 mm.

In size and structural details including the textured enamel, this tooth closely approximates the few known upper canines (more specifically, the deciduous canine) of the tillodont *Esthonyx* from the Wasatchian of western North America (e.g., UM 96053, USGS 10258, USNM 495050, all from the Willwood Formation of the Bighorn Basin, Wyoming). *Esthonyx* upper canines differ from the Fisher/Sullivan tooth, however, in being more robust labiolingually and in having a prominent vertical ridge near the middle of the lingual side of the tooth. USGS 10258 contains a deciduous (= "milk") canine, which is not as thick labiolingually and has a much weaker vertical ridge. It is quite similar, though not identical, to the Fisher/Sullivan tooth. Almost identical, however, is an isolated right upper canine (USNM 495049) recently recovered from the Willwood Formation and believed to represent *Esthonyx*. Size and morphology substantially restrict the taxa the Fisher/Sullivan tooth could represent, and of known Wasatchian mammals it resembles *Esthonyx* more closely than any other.

*Esthonyx* has not been previously reported from east of the Rockies in North America, but closely related tillodont genera are known from the early Eocene of western Europe (Baudry, 1992). Moreover, as noted above, a closely related trogosine tillodont from the middle Eocene of New Jersey is one of the few Eocene mammals known from eastern North America. Tillodonts have no living relatives and are still among the most enigmatic Early Tertiary mammals. Heavy tooth wear and enlarged incisors, supplemented by scattered skeletal remains, suggest that their diet consisted of roots,

tubers, or other coarse vegetation which they excavated with their clawed forelimbs (Gingerich and Gunnell, 1979; Coombs, 1983).

A second mammal tooth, also found by Michael Folmer, is the buccal half of a right upper molar, probably representing a tapiromorph perissodactyl (USNM 494880, Figure 3A). Unlike the canine, this tooth is heavily water-worn, indicating a long period or distance of hydraulic transport. Recognizable are the two principal external cusps, the paracone and metacone, preceded by a prominent, slightly lower parastyle. It is very similar in form to *Homogalax* (for example, USGS 1142, Figure 3B), but differs in having a short shelf or cingulum on the anterobasal surface of the parastyle. *Homogalax* is a basal tapiromorph (=moropomorph) from the early Eocene of the Rocky Mountain region. It is the sister taxon of tapirs, rhinos, and chalicotheres (Hooker, 1989; Prothero & Schoch, 1989), and appears to be among the most primitive of all perissodactyls (Rose, 1996). Like all perissodactyls, *Homogalax* was herbivorous, and transverse crests on the molars indicate a somewhat more folivorous diet than in its contemporary, the dawn horse *Hyracotherium*.

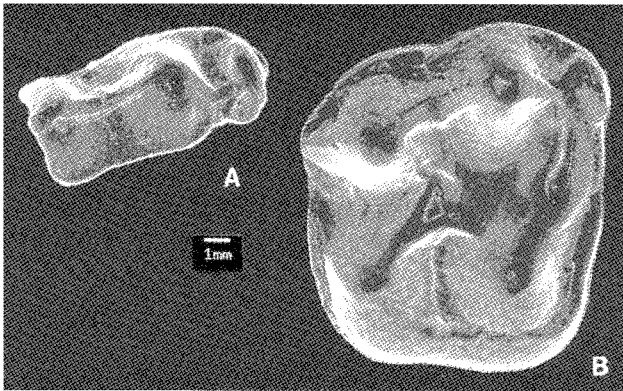


Figure 3. A, Buccal part of upper right molar of a tapiromorph perissodactyl (USNM 494880); B, Right M<sup>2</sup> of the tapiromorph *Homogalax* from the Willwood Fm., Bighorn Basin, Wyoming (USGS 1142).

The fourth mammal discovery from the Fisher/Sullivan site, made by Ron Keil, is a left lower premolar, probably P<sub>3</sub>, closely similar in size and structure to that of the pantolestid *Palaeosinopa* (USNM 495156, Fig. 4). It is elongate, buccolingually narrow, and simple, with a single tall central cusp and a small, low talonid cusp; an anterior cuspule was probably present but is broken away. As preserved, it measures 3.0 mm long and 1.5 mm wide. Pantolestids were archaic insectivores that are believed to have been carnivorous semiaquatic animals (e.g., Matthew, 1909; Pfretzschner, 1993).

Just prior to this volume going to press, three additional mammalian fossils were recovered in screen-washed concentrate from the Fisher/Sullivan site. The most significant of these is the first mammal jaw from this site, discovered by Ron Keil in December 1998. It is a fragment of a very small

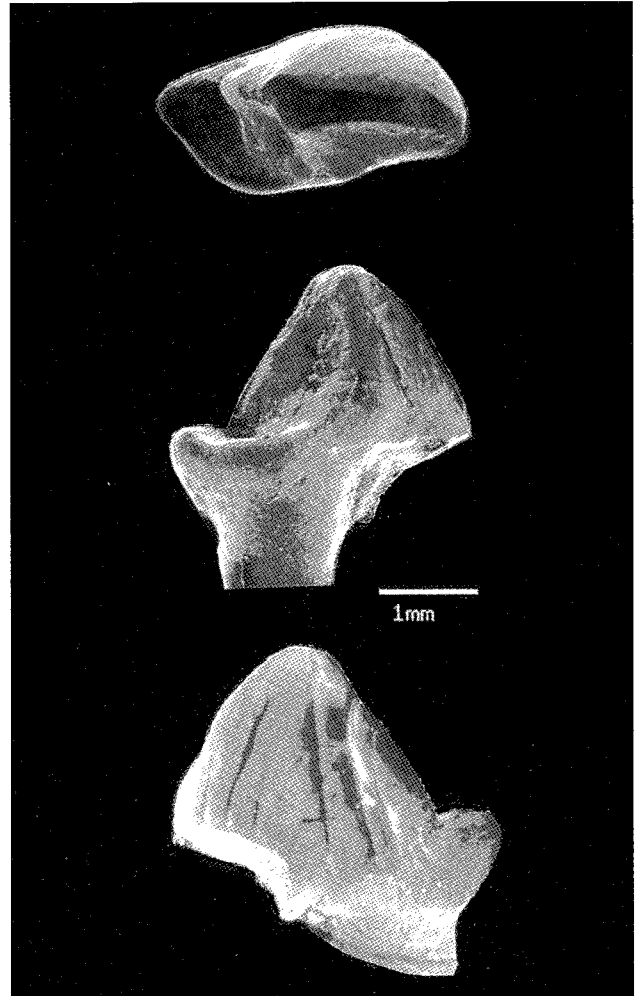


Figure 4. Occlusal, lingual, buccal views of a left lower premolar (P<sub>3</sub>?, USNM 495156), cf. *Palaeosinopa* species.

right dentary containing well-preserved P<sub>2-4</sub> of a nyctitheriid insectivoran (USNM 495290, Figure 5). It resembles known Paleocene-Eocene Nyctitheriidae from the Western Interior, particularly *Leptacodon* and *Plagioctenodon* (Krishtalka, 1976; Bown and Schankler, 1982), in having simple, two-rooted P<sub>2</sub> and P<sub>3</sub>, and a semimolariform P<sub>4</sub> with a low, anteriorly displaced paraconid and a well-developed, basined talonid. It differs from these and most other nyctitheriids, however, in several subtle details. P<sub>3</sub> is slightly taller than P<sub>2</sub>, whereas in most other nyctitheriids P<sub>2</sub> is slightly larger and taller than P<sub>3</sub>. P<sub>4</sub> of USNM 495290 has a weaker, lower paraconid than in most other nyctitheriids, and a lower entoconid that is posterolingual to the hypoconid, rather than the high, anteriorly shifted entoconid seen in other nyctitheriids. The hypoconulid is centrally located, not closer to the hypoconid as is more typical in nyctitheriids. These features suggest that the Fisher/Sullivan site nyctithere is generically and specifically distinct from known forms. Formal description is deferred pending more thorough study. Measurements of USNM 495290 are: P<sub>2</sub> length = 0.7 mm, breadth = 0.3 mm; P<sub>3</sub> length = 0.8 mm, breadth = 0.4 mm; P<sub>4</sub> length = 1.1 mm, trigonid breadth = 0.5 mm, talonid breadth = 0.5 mm.

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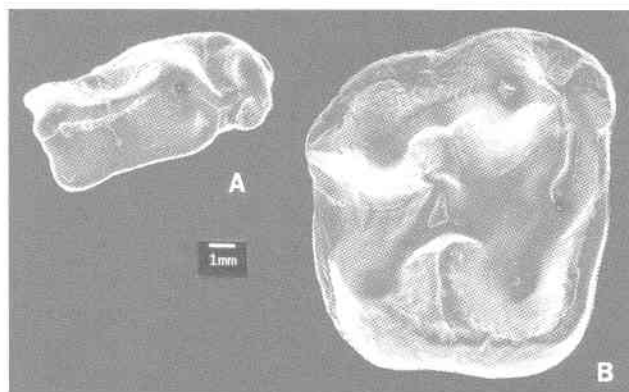


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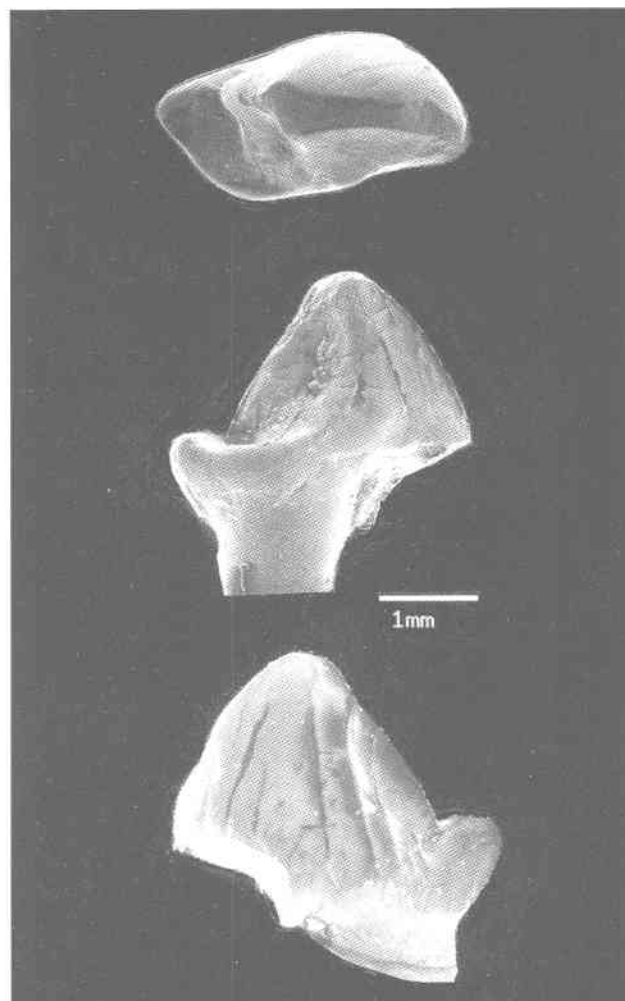


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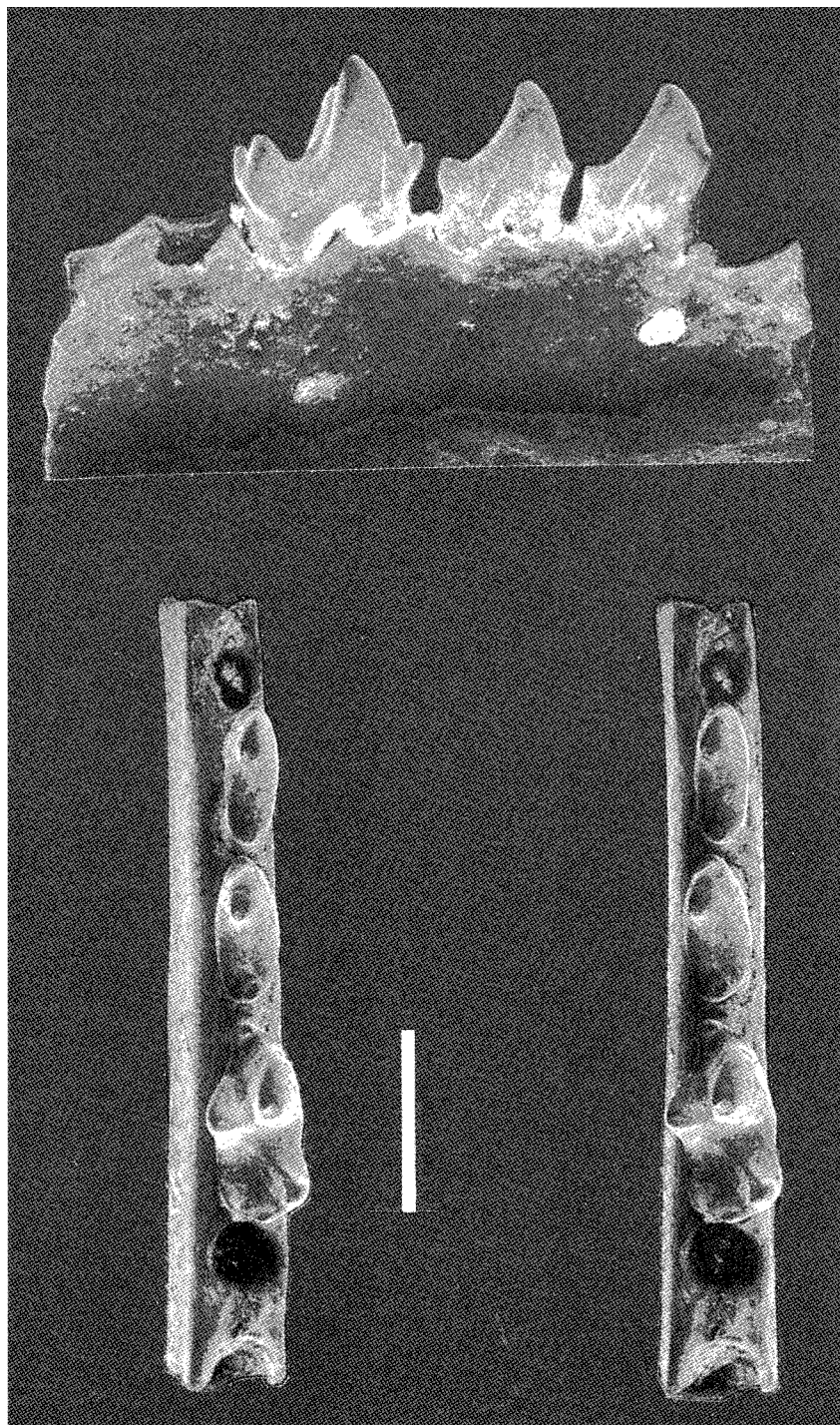


Figure 5. Right dentary with  $P_{2-4}$  of a nyctitheriid insectivoran (USNM 495290) in lateral view (above) and occlusal view (stereopair, below). Scale bar is 1 mm.

The other two new specimens are isolated teeth. A water-worn upper premolar (USNM 495293) found by Mike Folmer compares most closely with right the  $P^4$  of an early Eocene miacid Carnivora (Figure 6). It particularly resembles  $P^4$  of *Oodectes herpestoides* and some specimens of *Vulpavus* in having little or no distinct parastyle, a small and low protocone, and a relatively short metastyle blade (= postparacrista). How much of this morphology resulted

from the heavy abrasion is difficult to judge, hence more precise identification is not attempted here. The tooth is smaller than  $P^4$  of the miacids mentioned, measuring 3.3 mm long on the buccal border, which is chipped distally, and 2.6 mm in transverse width.

Another isolated tooth, found by Ron Keil, was received the same day this paper was sent to be set for proofs. It is a left  $M^2$  of a hyopsodontid condylarth (USNM 495294, Figure 7), similar to the abundant early Eocene *Hyopsodus* but with a less continuous ectocingulum and a smaller, less lingual hypocone than is typical in that genus. Its dimensions are 2.9 mm long by 4.1 mm wide.

This last new specimen brings to seven the number of mammalian taxa represented at the Fisher/Sullivan site. They are taxonomically distributed as follows:

#### Insectivora

##### Nyctitheriidae

genus and species unidentified, possibly new

#### ?Pantolestia

##### ?Pantolestidae

cf. *Palaeosinopa* sp.

#### Carnivora

##### Miacidae

genus and species indeterminate

#### Tillodontia

##### Esthonychidae

cf. *Esthonyx* sp.

#### Condylarthra

##### Hyopsodontidae

cf. *Hyopsodus* sp.

#### Perissodactyla

##### Tapiromorpha

##### Isectolothidae

aff. *Homogalax* sp.

#### ?Rodentia

##### ?Ischyromyidae

genus and species indeterminate

### SUMMARY

Fragmentary mammalian remains from the Fisher/Sullivan site — despite their preservation in marine sediments — provide a tantalizing first glimpse of an eastern terrestrial fauna similar to that known from early Eocene intermontane basins of western North America. The presence of seven different taxa, including teeth closely resembling those of the tillodont *Esthonyx*, the perissodactyl *Homogalax*, the pantolestid *Palaeosinopa*, and the condylarth *Hyopsodus*, are strongly suggestive of Wasatchian age.

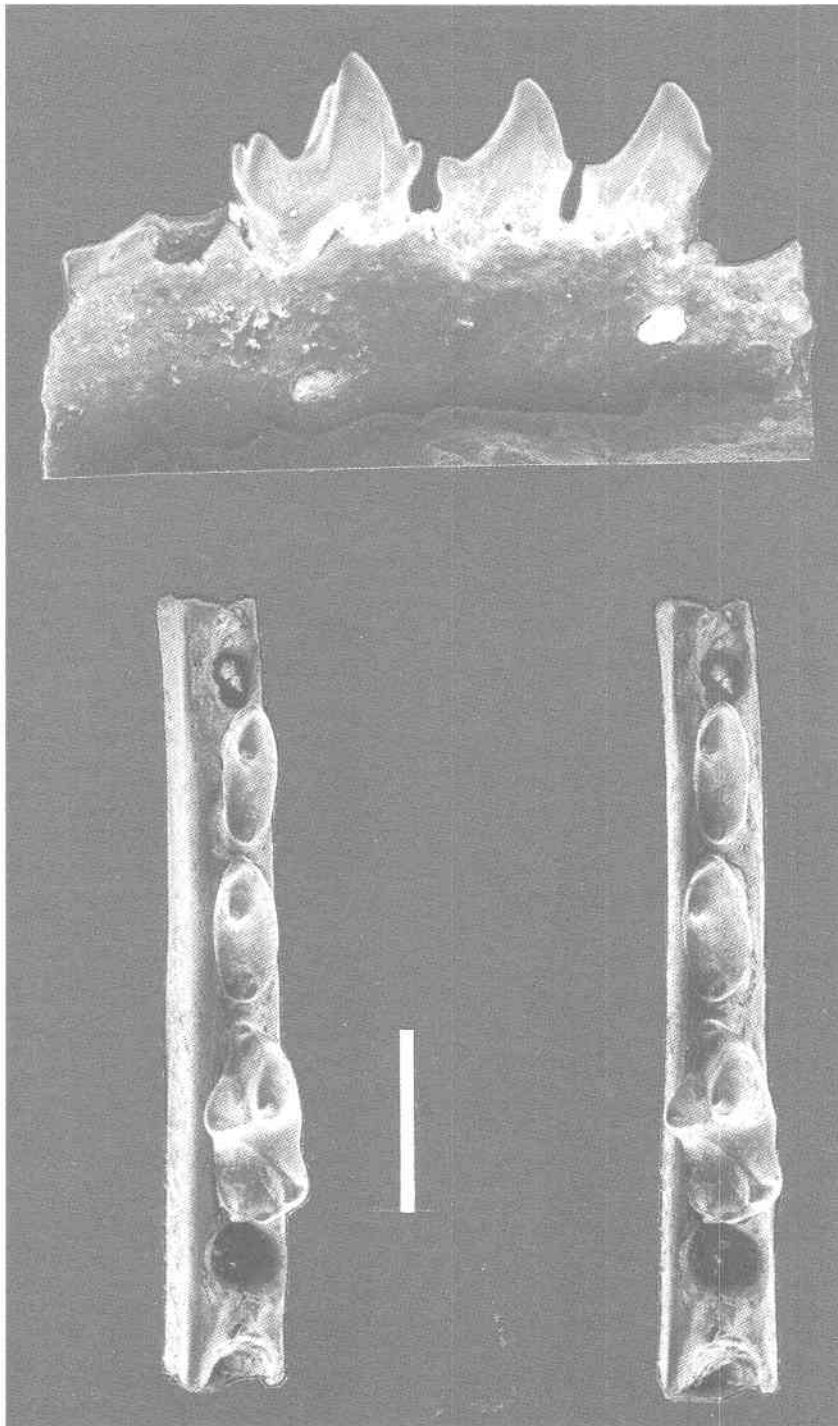


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#### Tillodontia

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#### Condylarthra

##### Hyopsodontidae

cf. *Hyopsodus* sp.

#### Perissodactyla

##### Tapiromorpha

##### Isectolothidae

aff. *Homogalax* sp.

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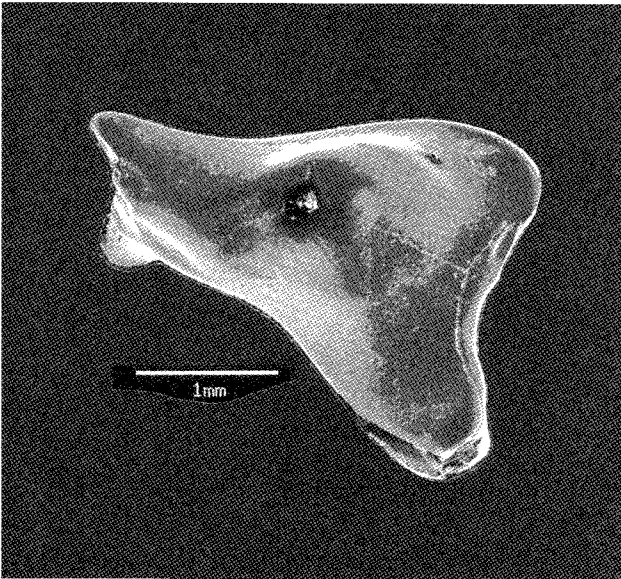


Figure 6. Right P<sup>4</sup> of a miacid carnivoran (USNM 495293).

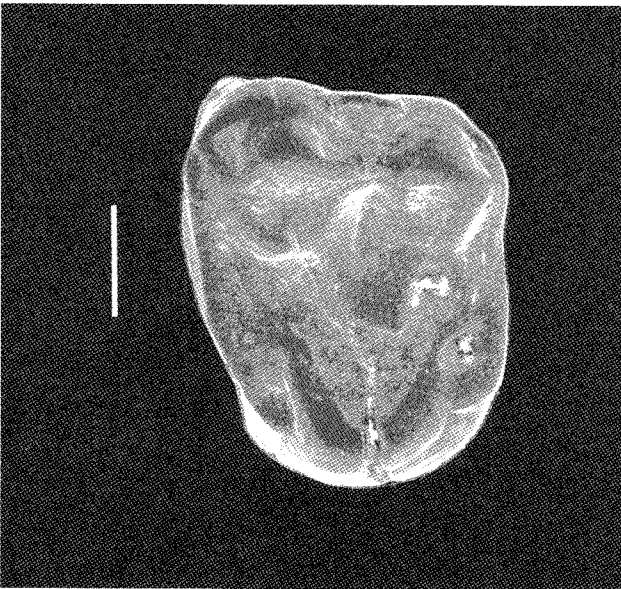


Figure 7. Left M<sup>2</sup> of a hyopsodontid condylarth (USNM 495294). Scale bar is 1 mm.

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#### REFERENCES

- Baudry, M. 1992. Les tillodontes (Mammalia) de l'Éocène inférieur de France. *Bulléin du Muséum National d'Histoire Naturelle*, Paris, 4<sup>e</sup> sér., 14, section C, no. 2: 205-243.
- Beard, K.C., and A.R. Tabrum. 1991. The first early Eocene mammal from eastern North America: an omomyid primate from the Bashi Formation, Lauderdale County, Mississippi. *Mississippi Geology* 11(2): 1-6.
- Beard, K.C., M.R. Dawson, and A.R. Tabrum. 1995. First diverse land mammal fauna from the early Cenozoic of the southeastern United States: the early Wasatchian Red Hot local fauna, Lauderdale County, Mississippi. *Journal of Vertebrate Paleontology* 15(3) Abstracts: 18A.
- Bown, T.M., and D.M. Schankler. 1982. A review of the Proteutheria and Insectivora of the Willwood Formation (lower Eocene), Bighorn Basin, Wyoming. *U.S. Geological Survey Bulletin* 1523:1-79.
- Coombs, M.C. 1983. Large mammalian clawed herbivores: a comparative study. *Transactions of the American Philosophical Society* 73(7): 1-96.
- Gazin, C.L. 1953. The Tillodontia: an early Tertiary order of mammals. *Smithsonian Miscellaneous Collections* 121(10):1-110 + 16 plates.
- Gazin, C.L., and J.M. Sullivan. 1942. A new titanotherium from the Eocene of Mississippi, with notes on the correlation between the marine Eocene of the Gulf coastal plain and continental Eocene of the Rocky Mountain region: *Smithsonian Miscellaneous Collections* 101(13):1-13.
- Gingerich, P.D., and G.F. Gunnell. 1979. Systematics and evolution of the genus *Esthonyx* (Mammalia, Tillodontia) in the early Eocene of North America. *Contributions from the Museum of Paleontology, University of Michigan* 25 (7): 125-153.
- Hooker, J.J. 1989. Character polarities in early perissodactyls and their significance for *Hyracotherium* and infraordinal relationships; pp. 79-101 in *The Evolution of Perissodactyls* (D.R. Prothero and R.M. Schoch, eds.), Oxford Univ. Press, New York.
- Krishtalka, L. 1976. North American Nyctitheriidae (Mammalia, Insectivora). *Annals of Carnegie Museum* 46:7-28.
- Leidy, J. 1868. Notice of some remains of extinct pachyderms. *Proceedings of the Academy of Natural Sciences*, 1868: 230-233.
- Matthew, W.D. 1909. The Carnivora and Insectivora of the Bridger Basin, Middle Eocene. *Memoirs of the American Museum of Natural History* 9 (6): 289-567.
- Pfretzschner, H.-U. 1993. Muscle reconstruction and aquatic locomotion in the middle Eocene *Buxolestes piscator* from Messel near Darmstadt. *Kaupia Darmstädter Beiträge zur Naturgeschichte* 3: 75-87.
- Prothero, D.M., and R.M. Schoch. 1989. Origin and evolution of the Perissodactyla: summary and synthesis; pp. 504-529 in *The Evolution of Perissodactyls* (D.R. Prothero and R.M. Schoch, eds.), Oxford Univ. Press, New York.

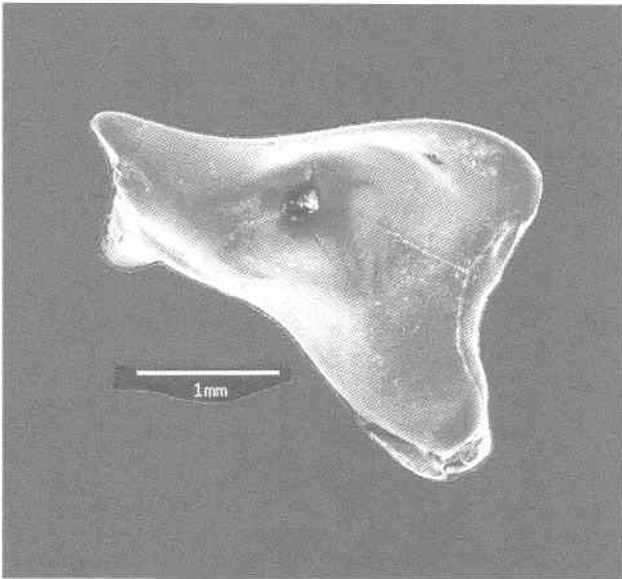


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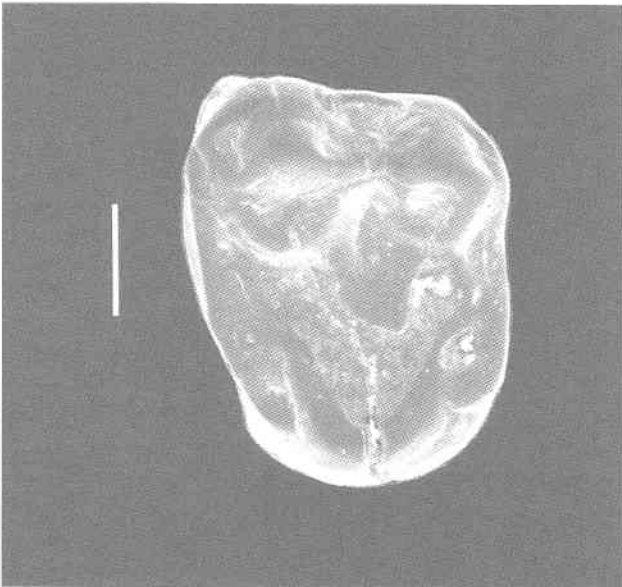


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- Pfretzschner, H.-U. 1993. Muscle reconstruction and aquatic locomotion in the middle Eocene *Buxolestes piscator* from Messel near Darmstadt. *Kaupia Darmstädter Beiträge zur Naturgeschichte* 3: 75-87.
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Rose, K.D. 1996. Skeleton of early Eocene *Homogalax* and the origin of Perissodactyla. *Palaeovertebrata*, vol. jubil. D.E. Russell (M. Godinot and P.D. Gingerich, eds.), 25: 243-260 + 1 plate.

Savage, D.E., and D.E. Russell. 1983. *Mammalian Paleofaunas of the World*. Addison-Wesley Publishing Company, Reading, Massachusetts. 432 pp.

Schiebout, J.A. 1979. An overview of the terrestrial Early Tertiary of southern North America--fossil sites and paleopedology. *Tulane Studies in Geology and Paleontology* 15: 75-93.

Schoch, R.M. 1985. Preliminary description of a new late Paleocene land-mammal fauna from South Carolina, U.S.A. *Postilla* 196: 1-13.

Schoch, R.M. 1998. Late Paleocene land-mammals from the Williamsburg Formation (Black Mingo Group) of South Carolina; pp. 229-245 in *Paleobiology of the Williamsburg Formation (Black Mingo Group; Paleocene) of South Carolina, U.S.A.* (Albert E. Sanders, ed.), *Transactions of the American Philosophical Society* 88(4): 1-276.

Simpson, G.G. 1932. A new Paleocene mammal from a deep well in Louisiana. *Proceedings of the U.S. National Museum* 82: 1-4.

Westgate, J.W. 1988. Biostratigraphic implications of the first Eocene land-mammal fauna from the North American coastal plain. *Geology* 16: 995-998.

Westgate, J.W. 1990. Uintan land mammals (excluding rodents) from an estuarine facies of the Laredo Formation (Middle Eocene, Claiborne Group) of Webb County, Texas. *Journal of Paleontology* 64: 454-468.

## PART 8. FOSSIL FRUIT AND SEED FLORA FROM THE EARLY EOCENE FISHER/SULLIVAN SITE

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Department of Geological Sciences  
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### ABSTRACT

A small fruit and seed flora of early Eocene age (NP 11; 56.5 to 55.5 Ma) is reported from the Potapaco Member of the Nanjemoy Formation, eastern Virginia, U.S.A. Nine taxa are identifiable to genus (*Canarium*, *Beckettia*, *Wetherellia*, *Iodes*, *Tinospora*, *Nyssa*, *Symplocos*, *Ampelopsis*, *Vitis*); all are found in the early Eocene London Clay of southern England and six are present in the middle Eocene Nut Beds flora of the Clarno Formation of Oregon, U.S.A. In addition, a fruit of *Nypa* is described from nearby and slightly younger sediments of the Nanjemoy Formation in Maryland. Together, these occurrences emphasize the probable importance of the early Eocene North Atlantic land bridge in the evolution of the flora and fauna of the Northern Hemisphere.

### INTRODUCTION

The similarity at the generic level between the flora of southeastern Asia and southeastern North America, is a long recognized pattern in the phytogeography of the modern Northern Hemisphere (Gray, 1840, 1878; Graham, 1972). This similarity is shared to a lesser degree with floras of western North America, the mountains of Eastern Mexico, and the Caucasus mountains of Central Asia. Exploration of the fossil record reveals that this pattern has its roots in the Early Tertiary, when a burst of angiosperm evolution coincided with the rapid spread of new taxa, resulting in the widespread distribution of many angiosperm families and genera that survive in different regions of the Northern Hemisphere to the modern day. This dissemination was made possible by three factors. First, the climates of the Early Tertiary were considerably warmer than those of the present, allowing frost-free winters to approximately 60° - 70° north paleolatitude (Tiffney, 1985a, 1994a). Second, two land bridges linked the Old and New Worlds at this time. The Bering Land Bridge lay at approximately 75 degrees North Paleolatitude (Tiffney, 1985b), permitting passage of cool and winter-dark tolerant plants. The North Atlantic Land Bridge provided a link between eastern Canada and Northwestern Europe via southern Greenland at approximately 55 degrees paleolatitude (Tiffney, 1985b). This bridge was at a low enough latitude to provide winter sun and presumably passage to frost-intolerant plants (Tiffney, 1994a). Finally, both angiosperms and vertebrate dispersal agents were radiating into the ecological void caused by the disturbance at the Cretaceous-Tertiary boundary, thus the newly evolving plants were rapidly dispersed by newly evolving and migrating vertebrates (Tiffney, 1984), allowing a rapid geographical spread of

new taxa throughout the Northern Hemisphere, regardless of their point of geographic origin.

The result of this concatenation of events was the development of a hemispheric-wide flora which Wolfe (1975, 1985) has titled the Boreotropical Flora (see also Lavin and Luckow, 1993). This plant assemblage was dominated by families and genera that today grow in warm-temperate and subtropical, frost free, climates, although it also included lineages whose descendants evolved increasing cold-tolerance through the Tertiary. The majority of these taxa were probably evergreen angiosperms; thus the vegetation they formed would appear green year round. The widespread nature of the Boreotropical Flora is evidenced by the generic and sometimes specific-level similarity of such widely separated Eocene floras such as those of Europe (e.g., the London Clay of Southern England: Chandler, 1964; Collinson, 1983; the Weisselster Basin of Germany: Mai and Walther, 1985; the Pasekovo flora of Russia: Vickulin, 1996) on the one hand, and various Eocene floras of Western North America (e.g., the Clarno Nut Beds flora: Manchester, 1994; the Princeton Chert: Erwin and Stockey, 1994; the Eocene floras of the Northern Sierra: Tiffney & Haggard, 1995; the Sand Draw Flora of Wyoming: Tiffney, 1996) on the other.

As a result of the climatic deterioration of the later Tertiary, the components of the Boreotropical Flora became segregated. Frost-intolerant taxa became increasingly restricted to more southerly and protected sites, while the flora of the intervening areas evolved a temperate aspect. Quaternary glaciations completed this process, enforcing the present patterns of flora and vegetation upon the Northern Hemisphere, including the disjunct distribution of frost-intolerant taxa in southeastern Asia and North America (Tiffney, 1985a).

The widespread nature of the Boreotropical Flora, and the apparent importance of the North Atlantic Land Bridge in its spread, leads to the prediction that the Eocene flora of eastern North America should have been similar to that of Europe and western North America. The problem is that there are very few reports of Tertiary age plant remains from the eastern seaboard of North America northeast of the Mississippi Embayment. Berry (see LaMotte, 1952) described many individual specimens, but, in general, these identifications require re-confirmation. Mazer and Tiffney (1982) reported fruits of *Wetherellia* Bowerbank and *Palaeowetherellia* Chandler, two common London Clay genera, from the early Eocene Nanjemoy Formation of Virginia. Gee (1990) reported fruits of the palm *Nypa* Steck

from the Eocene of Texas, again suggesting a North Atlantic link to the European Eocene where *Nypa* is a common constituent of coastal floras. The early Miocene flora of the Brandon Lignite of Vermont (Tiffney, 1994b) contains many Boreotropical elements, but is temporally isolated from the presumed period of exchange in the Eocene. Studies of pollen floras (Frederiksen, 1995) support the interpretation that Boreotropical taxa were present in the Eocene of Atlantic North America. However, pollen does not provide the precision of identification necessary to allow comparison of taxa from widely separated geographic localities. The Eocene floras of the Mississippi Embayment (Dilcher, 1973) reflect a more Central and South American heritage, although there is much research yet to be done and a significant Boreotropical influence may yet be demonstrated.

The lack of described Eocene floras from Atlantic North America is exacerbated by increasing urbanization. This has placed many potential fossil sites under asphalt, or in the backyards of unfriendly land owners. For this reason, the discovery of the Fisher/Sullivan site is of great value in opening a window to the composition of the Early Tertiary flora of the Atlantic coastline. While the flora reported here is small, it includes several taxa that are common in both European and western North American Eocene floras, suggesting that the model of the spread of the Boreotropical Flora via the North Atlantic Land Bridge is a viable hypothesis. It is to be hoped that the continued efforts of amateur and professional collectors at this site will generate a diverse flora of which the present paper provides only an initial report.

### GEOLOGIC SETTING

The Fisher/Sullivan site is located in the bed of an unnamed tributary of Muddy Creek in eastern Stafford County Virginia (77° 22' 02" West, 38° 17' 06" North). The flora is apparently derived from "Bed B" (Ward, 1985; Weems and Grimsley, this volume) of the Potapaco Member of the Nanjemoy Formation. The age of "Bed B" is placed within calcareous nannofossil zone NP11 (Gibson and Bybell, 1991) which is approximately 56.5 to 55.5 Ma (Harland, et al., 1990), corresponding to the early Ypresian stage of the early Eocene. There is a faint possibility that some of matrix from which the plants were collected was derived from the "Bed A" of the Potapaco, possibly extending the time range of the flora into slightly older sediments.

The plant remains are associated with a diverse array of marine and terrestrial vertebrates (cf., other articles in this volume). All have been recovered from a narrow layer within glauconitic, fine-grained, marine sands with admixed larger quartz grains and pebbles ranging up to 1 cm in diameter. The paleocoastline of Virginia lay approximately 13 km west of the site (Weems and Grimsley, this volume). Presumably terrestrial remains rafted out from streams and rivers, in a setting not dissimilar to that of the London Clay (Allison, 1988).

### FOSSIL MATERIAL

The fossil material described here was largely collected by amateur paleontologists using the screen washing techniques of vertebrate paleontology. The fossils are preserved as original organic material, as original organic material infiltrated by pyrite, or as organic material entirely replaced by pyrite. The quality of the preservation varies, but is generally good, and cellular-level patterns may be discerned on several specimens. With time, the pyrite-infiltrated specimens show cracking resulting from dehydration and/or the effects of acid release and require storage in glycerine.

### MATERIALS AND METHODS

The fossils were examined with a Nikon SMZ 10 dissecting microscope; photographs were taken on Kodak Tmax 100 film using a Nikon HFX-II automatic exposure system attached to the dissecting scope.

### SYSTEMATICS

The taxa recovered from the Fisher/Sullivan flora varied in the numbers of representatives of each morphology and the quality of their preservation. Some taxa possessed enough characters that they were clearly identifiable to genus. In some cases, these proved indistinguishable from previously described fossils, and were accordingly placed in pre-existing species. In other cases, they were clearly different from previously described fossil species and were thus placed in new species. In several cases, however, the material was too poorly preserved or too limited to warrant specific identification; such specimens are identified only to genus until further material is collected. The composition of the flora is summarized in Table 1, which includes the palm *Nypa* from the slightly younger Woodstock Member of the Nanjemoy Formation in Maryland.

All specimens are deposited in the collections of the Department of Paleobiology, National Museum of Natural History (USNM), Smithsonian Institution.

### SYSTEMATIC DESCRIPTIONS

#### Family Burseraceae Genus *Canarium* L.

The living genus involves about 75 species (Willis, 1973; Mabberley, 1987) of trees, shrubs and "pseudolianes" (Leenhouts, 1959) which generally inhabit low elevation primary and secondary rainforests in monsoonal climates. Three species are native to Africa, Madagascar and the Mauritius, two to Australia, and the remainder occur from India east through Melanesia (Leenhouts, 1959).

Fossil fruits of *Canarium* have been reported from the Early Tertiary of Europe (Gregor and Goth, 1979). These

Table 1. Paleo- and neogeographic affinities of the identified taxa from the Fisher/Sullivan Flora. London Clay = taxon found in the early Eocene London Clay Flora; Clarno = taxon found in the middle Eocene Clarno Nut Beds Flora. Distributional data largely from Willis (1973) and Mabberley (1987); see text for further discussion.

FAMILY	GENUS	HABIT	MODERN GEOGRAPHIC AFFINITY	London Clay	Clarno
Burseraceae	<i>Canarium</i>	Evergreen tree	Tropical Asia and Africa	Yes	No
Cornaceae	<i>Beckettia</i>	unknown	Extinct genus	Yes	No
Euphorbiaceae	<i>Wetherellia</i>	unknown	Extinct genus, probably a mangrove	Yes	No
Icacinaeae	<i>Iodes</i>	Large vine or liane	Tropical Asia and Africa	Yes	Yes
Menispermaceae	<i>Tinospora</i>	Large vine or liane	Tropical Eastern Asia	Yes	Yes
Nyssaceae	<i>Nyssa</i>	Deciduous tree	Eastern North America, Central America and Eastern Asia	Yes	Yes
Symplocaceae	<i>Symplocos</i>	Shrubs, rarely trees	Old and New World tropics and subtropics	Yes	Yes
Vitaceae	<i>Vitis</i>	Large vine or liane	Both temperate to subtropics, Northern Hemisphere	Yes	Yes
	<i>Ampelopsis</i>	Vine		Yes	Yes
Palmae	<i>Nypa</i>	Mangrove palm	Southeast Asia to Australia	Yes	No

authors also note a “personal communication” from T. Tanai that *Canarium* is known from a Miocene fruit from Honshu, Japan. Raubeson and Tiffney (unpublished) identify a *Canarium* fruit from the early middle Eocene Wagon Bed formation of Wyoming. Leaves closely compared with *Canarium* have been described from North American floras (Hickey, 1977; Myers, 1990).

*Canarium parksii* sp. nov.  
Plate One, Figures 1, 2.

**Material:** Thirteen fully to partially intact fruits, several fragments. The majority of fossils are pyritized and difficult to section, while the remainder are a combination of pyrite and original organic matter that disintegrates with prolonged exposure to air.

The type specimen is assigned USNM #495826 and was collected by Mr. Thomas Parks. The remaining 12 intact fruits are assigned USNM #495827 through 495838, and the fragments are collectively assigned USNM #495839. The remaining specimens were collected by Mr. Thomas Parks, Mr. Gary Grimsley and Mr. Michael Folmer.

**Derivation of name:** The specific name honors Mr. Thomas Parks of the Maryland Geological Society, who collected and made available for study many specimens from the Fisher/Sullivan site.

**Description:** The fruits average 7.45 mm long (N =12; maximum 9.0 mm, minimum 5.8 mm) and 4.2 mm in widest diameter (N=12; widest 5.6 mm, narrowest 2.5 mm). They are tear-drop shaped, with an attenuated apex spreading to a

greatest diameter roughly 2/3 of the way to the base of the fruit. The base is marked by a small attachment scar. The fruits are composed of a star-like central axis with two to four embayments. Nested within each embayment is a unilocular pyrene, each pyrene dehiscent by a valve which opens from the top of the pyrene to approximately 80% of its length towards the base. The external face of each pyrene may be domed outwards or collapsed. The fruits are most commonly trimerous. Occasionally, two pyrenes develop fully, the third being much reduced and presumed abortive. In one case it appears that there are three mature pyrenes and a fourth reduced and abortive one. Each pyrene is demarcated by a surrounding line indicating its juncture to the central axis. In well-preserved specimens, a second line within the pyrene margin indicates the location of the dehiscence valve. While the majority of the pyrenes remain attached to the central fruit axis, in a few occasions it appears that the entire pyrene is missing, leaving a corresponding depression in the face of the fruit axis.

The pyrene locule contains a single, compressed, tear-drop-shaped, smooth seed possessing an elongate apex. It is slightly flattened on the dorsal (outer) surface and rounded on the ventral (inner). It would be inappropriate to try to distinguish the raphe, chalaza and micropyle given the poor quality of preservation. However, it is apparent that the point of seed attachment is approximately in the middle of its ventral face. Cellular preservation is poor; in one seed the surface was composed of polygonal cells.

**Discussion:** The character of valvate pyrenes, retained within a multi-rayed axis, is distinctive of the Burseraceae. Within the family, the proliferation of the axis to form a

multi-armed receptacle embracing the pyrenes is distinctive of *Canarium* (Lam, 1932; Leenhouts, 1956, 1959). While living *Canarium* fruits are generally much larger than the fossil, some are of a similar size (e.g., *C. acutifolium* (DC) Merr. var *acutifolium*, *C. asperum* Benth.; Leenhouts, 1956). Further, the exposure of the pyrenes and the central axis in the fossil indicates that the exocarp is missing, meaning that the measurements provide a minimum size for the fossils.

The fossils also closely resemble the London Clay fossil *Tricarpellites communis* Reid and Chandler (Reid and Chandler, 1933). Reid and Chandler noted that *T. communis* was very similar to *Canarium*, but distinguished the two on the basis of the characters of the raphe, chalaza, shape of the dehiscent valve and tendency of the fossil to split into separate units. The question arises, is the Virginia fossil best allied with *T. communis* or *Canarium*?

Relative to *T. communis*, the Virginia material is more attenuated at the apex while the European species is rounded. The Virginia material does not tend to break into pyrenes like the European material, although some American specimens display loss of one pyrene from the fruit. The pyrene valves in the European material are 1/3 to 1/2 the length of the carpel; in the Virginia material the valve is much longer, up to 4/5 or more of the pyrene length. Finally, in the Virginia material the point of vascular attachment is approximately 1/2 of the way along the length of the seed, rather than 1/5 of the way down from the apex as in *T. communis*. In all these distinctions save shape, the Virginia fossils fall closer to *Canarium* than to *T. communis*, suggesting that the Virginia material is best assigned to *Canarium*. This distinction may have limited significance. Reid and Chandler frequently erected extinct genera on very minor differences between the extant and fossil material. In a careful revision, it is likely that *Tricarpellites communis* would be regarded as a species *Canarium*.

### Family Cornaceae

#### Genus *Beckettia* Reid and Chandler

Reid and Chandler (1933) recognized a diversity of syncarpous fruits of the Cornaceae in the London Clay flora. In describing these fossils, they opted to erect several new genera to encompass variations in fruit structure, size and locule number, including *Lanfrancia* Reid and Chandler and *Beckettia* Reid and Chandler. In 1961, Miss Chandler added a third similar genus, *Portnallia* Chandler. Mai (1993) argued that all three genera were essentially similar, and subsumed *Lanfrancia* and *Portnallia* into *Beckettia*, recognizing four extinct species. The critical characters of *Beckettia sensu lato* include the presence of two to four locules with shallow dorsal infolds, arranged around a common, largely parenchymatous axis. The individual locules dehisce by dorsal germination valves. In general these fruits were globose to subglobose, but occasional ovoid specimens are recognized. To date the genus is known from the uppermost Cretaceous of Europe (Knobloch and

Mai, 1986; Mai, 1993) and the early Eocene of England (Reid and Chandler, 1933; Chandler, 1961; Collinson, 1983).

#### *Beckettia* ? species

Plate One, Figures 3, 4.

**Material:** One fruit, involving original organic matter, sediment and pyrite; very poorly preserved. The specimen is assigned USNM #495840 and was collected by Mr. Michael Folmer.

**Description:** Remains 9.1 mm long, about 3.0 mm wide on the two preserved faces. The fossil consists of two carpels, arranged around a central axis and set off from each other by about 120 degrees. The remaining space suggests that a third carpel was present, but is now lost. The central axis has been almost completely eroded and replaced by pyrite and sediment, but retains scraps of embedded organic matter. Each of the two remaining carpels is elongate and widest near its apical end, the apex taking the form of a broad, gently-tipped triangle. The carpel contracts towards the base, terminating in a gentle, but much smaller triangle. The dorsal surface of each carpel is broadly C-shaped in cross section. The surface of the carpel is covered by a thin layer of longitudinally-elongate sclereids.

**Discussion:** The character of three separate carpels, each with a broad linear depression running down its length, is suggestive of the Cornaceae, and an apical view of the fossil is quite similar to that of *Beckettia* (*Portnallia*) *bognorensis* Chandler (Chandler, 1961, plate 28, figure 40), one of two species she recognized in this extinct genus.

The fruit of *Beckettia sensu lato* is composed of parenchyma, which was easily degraded to reveal and liberate the individual carpels. This would agree with the lack of organic preservation of the central axis in the Virginia fossil. The broad, low longitudinal depression is also in agreement with the locule shape observed in some species of *Beckettia*, although others tend to have deeper locular depressions (e.g., *B. mastixioides* Reid and Chandler; Mai 1993, text-figure 2). The shape of the Virginia fruit is perhaps a bit more elongate than is common in *Beckettia*, but some specimens of *Beckettia mastixioides* and *Lanfrancia subglobosa* illustrated by Reid and Chandler (1933, plate 25) approach the presumed shape of the Virginia fossil. The thin, woody, endocarp composed of fibrous cells described for *Beckettia bagnorensis* (Chandler) Mai is in agreement with the Virginia material. The sole reservation in this identification is that the Virginia material does not exhibit a clear zone of dehiscence indicative of a germination valve. This feature is often difficult to ascertain on endocarps of living and fossil Cornaceae, and thus may or may not be a problem.

*Triplascapha* Manchester (Manchester, 1994), a genus of undetermined higher affinities, is also quite similar in

many respects to *Beckettia bognoensis*. However, *Triplascapha* differs from the Virginia fossil in the following respects: it is substantially smaller, the carpels are much closer together, leaving less room in the central axis, and the exterior layer of the seed coat is equiaxial.

While the best judgement that can be made given the present data is that this fossil represents *Beckettia*, its single occurrence and poor preservation argue for caution, hence the “?” in the assignment. This identification should be taken as provisional, pending the discovery of further material.

**Family Euphorbiaceae?**  
**Genus *Wetherellia* Bowerbank**

*Wetherellia* is an extinct genus of fossil fruit commonly found in the early Eocene floras of southern England (Reid and Chandler, 1933; Chandler, 1961), northern Europe (Chandler, 1978), Maryland and Virginia (Mazer and Tiffney, 1982) and Mississippi (Call, Manchester, and Dilcher, 1993). The fruit is a spherical or subspherical, syncarpous capsule ranging from 3 mm to 24 mm in diameter. It consists of two to eight carpels arranged around a hollow (possibly pith-filled) central canal. The fruits frequently break into the individual carpels, which in turn dehisce loculicidally to reveal a single anatropous seed. The fruit wall is three layered, including a thin epicarp which is often lost, a mesocarp of equidimensional cells, and a thin endocarp of elongate fibers around the locules. Three species have been recognized (see Mazer and Tiffney, 1982 for a detailed synopsis), and a second genus from the Eocene of Egypt, *Palaeowetherellia* Chandler (Chandler, 1954) is closely related.

The family attribution of *Wetherellia* is not clear. Reid and Chandler (1933) initially suggested Linaceae. Mazer and Tiffney (1982) undertook an extensive search for comparable fruit morphologies in a wide range of living families. They concluded that *Wetherellia* is most similar to members of the Euphorbiaceae, but that it also had some similarities with fruits in the Meliaceae.

*Wetherellia marylandica* (Hollick) Mazer and Tiffney  
Plate One, Figures 5, 6, 7.

**Material:** Five fruits, three intact, one partial, one broken into its component carpels. All are largely organic, with infiltrating pyrites. The five fruits are assigned USNM #495841 through 495845 and were collected by Mr. Michael Folmer, Mr. Gary Grimsley and Mr. Ronald Keil.

**Description:** Spherical fruits, the smallest 9.65 mm in diameter, the largest 15.2 mm; the remaining fruits 14.5 mm, 14.5 mm and 10.7 mm in diameter. Each consists of six (in one case, five) carpels radially arranged around a central axis. The surface of the fruit is traversed by 12 (in the one case, 10) longitudinal lines representing the junctures of the individual carpels and the median (loculicidal) dehiscence

line of each carpel. The central axis is infilled with pyrite. In two fruits, the axis extends beyond the apex of the fruit and expands into a six-lobed structure, perhaps reflecting a style or stigma on the original fruit. The individual carpels are composed of a wide outer zone of apparently isodiametric cells, enclosing a narrow envelope of elongate fibers surrounding the locule. The fruits initially split between the carpels, liberating the carpels as separate cocci. They then split along the midline of each carpel to reveal a single, anatropous, lenticular, seed possessing a thin seed coat of black, reflective, polygonal cells. The vascular trace to the seed departs the central axis about one quarter of the distance below the fruit apex and is adherent to the ventral margin of the seed.

**Discussion:** *Wetherellia marylandica* is a spherical, syncarpous fruit 9.0 mm to 17.0 mm in diameter, consisting of two to six, most commonly four, loculicidal carpels. It is only slightly different from the common London Clays species, *W. variabilis* Bowerbank, and could be conspecific with the latter. Call, Manchester and Dilcher (1993) have found very similar fruits in early Eocene sediments in Mississippi which bridge between characters of both *W. marylandica* and of *W. variabilis* and the third English species, *W. dixonii* Chandler, suggesting that the three may represent a single, variable species.

The specimens described here conform to *Wetherellia marylandica* in all but two respects. The funicles in the Fisher/Sullivan fruits depart the main axis lower down than in the material described by Mazer and Tiffney (1982). The original material of *W. marylandica* was dominantly loculicidal while the Fisher/Sullivan site material is both septicidal and loculicidal. Both variations place the Fisher/Sullivan site material closer to *W. dixonii* and *W. variabilis*, and reinforce the suggestion that these taxa may represent variations within a single species (Call, Manchester and Dilcher, 1993).

The presence of *Wetherellia* reinforces the similarity of the Fisher/Sullivan flora to that of the London Clay. After *Nypa*, *Wetherellia* is the most common fossil in the London Clay (Reid and Chandler, 1933). *Nypa* (see below) is a mangrove palm that inhabits brackish water environments along coastlines in eastern Asia and Australia. Because the London Clay is a marine deposit, it only makes sense that coastal plants like *Nypa* should be common. Inverting this logic, it stands to reason that other numerically common elements of the flora quite likely represent coastal or mangrove taxa. While *Wetherellia* is not especially common in the Fisher/Sullivan flora, it was found in great numbers slightly higher in the Woodstock Member of the Nanjemoy Formation (Mazer and Tiffney, 1982), consonant with its occurrence in the London Clay flora and the interpretation that its source plant grew in coastal communities. This occurrence of *Wetherellia* is the oldest reported on the Atlantic coast, and is apparently coeval with its occurrence in the London Clay (Reid and Chandler, 1933; Chandler, 1961) and in the Mississippi Embayment (Call, Manchester, and Dilcher, 1993).

**Family Icacinaceae**  
**Genus *Iodes* Blume**

*Iodes* is a living genus of 14 (Willis, 1973) to 28 (Mabberley, 1987) species found from tropical Africa and Madagascar to Indomalaysia. The living plants are dioecious vines, lianes (large vines) or climbing shrubs, often climbing with tendrils. In Malaysia, many of the species inhabit forest margins or light-rich areas within the forest, although two are recorded as being found in primary forest, and one of these as a large liane (Sleumer, 1971). The African species appear similar in their range of stature and general ecology (e.g., Villiers, 1973).

Endocarps of *Iodes* commonly occur as fossils in the Early Tertiary floras of Europe (Knobloch and Mai, 1986) and western North America (Manchester, 1994) along with other Icacinaceous fruits (Manchester and Tiffney, 1993).

*Iodes multireticulata* Reid and Chandler  
 Plate One, Figures 8, 9.

**Material:** Two endocarps, both broken, one heavily pyritized. The carbonaceous endocarp (Plate one, figure 8) is assigned USNM #495846. The pyritized endocarp (Plate one, figure 9) is assigned USNM #495847. These were collected by Mr. Gary Grimsley and Mr. Michael Folmer.

**Description:** Endocarp subspherical, laterally flattened and bilaterally symmetrical, 4.0 to 4.5 mm high (chalazal end to hilum/micropyle), 4.5 to 5.0 mm wide, about 3 mm thick, enclosing a single locule. The apex is mildly attenuate. The endocarp surface is marked by a weak to strongly expressed reticulum of ribs. The areoles of the reticulum are approximately 0.6 to 0.8 mm in diameter. The plane of symmetry is marked by a slight rib on each margin; the rib on one margin being slightly larger than the rib on the other. The hilum and micropyle lie at one end, and the vascular trace passes at a long angle from the hilum through a canal in the thicker margin of the endocarp to its base, where it enters the locule cavity. This raphe is marked in one specimen by an open canal, and in the other by a trace of infilling pyrites. The fruit wall is about 0.3 mm thick. It is apparently three layered, an outer and inner layer of tangentially-elongate sclereids sandwiching an intermediate layer of larger cells; this latter layer appears to be of differential thickness and could be a preservational artifact. Both specimens are broken. At high magnification, the locule lining of both specimens is observed to bear widely spaced, elongate, narrow papillae.

**Discussion:** The characters of the surficial faceting, passage of the raphe through the testa, and the papillate locule lining allow a secure assignment (cf., Manchester, 1994) to *Iodes* Blume. The variation in the strength of the surficial sculpture and the thickness and composition of the wall of the two specimens leads one to consider recognizing two species, but

similar variation has been observed in both the London Clay (Reid and Chandler, 1933; Chandler, 1961) and Clarno (Manchester, 1994) specimens. As a result, one species is recognized. The best-preserved endocarp is very similar to *I. multireticulata*, first described and named from the early Eocene London Clay flora (Reid and Chandler, 1933; Chandler, 1961); the species has also been recognized from the middle Eocene Nut Beds flora of Oregon (Manchester, 1994). In the absence of data suggesting otherwise, the Virginia fossil is assigned to this species.

**Family Menispermaceae**  
**Genus *Tinospora* Miers**

The living genus *Tinospora* has nine species in Africa and Madagascar, and 23 in Asia, Australia and the Pacific islands (Forman, 1981). If *Odontocaryoidea* Miers is conspecific with *Tinospora* (Forman, 1981), this adds another approximately 30 species from South and Central America to the genus. However, this contention is not universally accepted. In either a restricted or broad sense, the genus is comprised of vines and lianes that occur in tropical evergreen and (in one case) deciduous forests; several species frequent littoral forests along coasts (Forman, 1981, 1986). The endocarps are distinctive, being approximate hemispheres, the flattened ventral surface bearing a weak to strong concavity or condyle that intrudes into the locule. The curved dorsal surface may be smooth, spinose, verrucose, rugulate or otherwise ornamented. Many species bear a median dorsal ridge of varying strength, which may be prolonged at the apex or base of the endocarp, and which may wrap around to the margins of the condyle on the ventral face.

*Tinospora* is a common component of Early Tertiary Boreotropical floras. Three species are known from the London Clay (Reid and Chandler, 1933; Chandler, 1961; Collinson, 1983) and one from the Lower Bagshot Beds (Chandler, 1962) of England. Two species are present in the Clarno Nut Beds flora of Oregon (Manchester, 1994), and *Tinospora*-like endocarps occur in the late Eocene Auriferous Gravels flora of California (Tiffney, unpublished). The tropical affinities of the genus are attested to by its apparent absence from cooler, Post-Eocene, floras.

*Tinospora folmerii* sp. nov.  
 Plate Two, Figures 1, 2.

**Material:** One endocarp, largely infiltrated with pyrite, but retaining the endocarp wall as carbon. The single specimen is assigned USNM #495848 and was collected by Mr. Michael Folmer.

**Derivation of name:** The specific name honors Mr. Michael Folmer of the Maryland Geological Society, who has collected and made available for study many specimens from the Fisher/Sullivan site.

**Description:** Hemispherical endocarp, 5.5 mm long, 4.0 mm wide and 2.0 mm thick. The arched dorsal surface bears a pronounced median ridge that extends beyond the margin of the endocarp as it passes around the apex and base. The lateral portions of the dorsal surfaces are marked by an anastomosing pattern of low but distinct ridges that create irregular polygons. The ventral surface is occupied by a depression, largely infilled with pyrite. The pattern of ridges from the dorsal surface dies out on the two lateral margins of the ventral depression. The dorsal ridge carries around the apex and base and extends into the ventral depression, disappearing beneath the pyrite filling. Where it has broken free of the underlying pyritic infilling, the endocarp wall is quite thin.

**Discussion:** The hemispherical shape with a dorsal ridge and surficial pattern, giving way to a ventral depression is characteristic of several genera of the Menispermaceae, tribe Tinosporeae. The size and shape of the endocarp, together with the specific characters of ornamentation, most closely match those observed in endocarps of living species of *Tinospora* (cf. illustrations in Forman, 1981, 1986). The only other similar endocarp belongs to the extinct form genus *Menispermicarpum* Chandler which differs by being dorso-ventrally flattened, and possessing ventrilateral ridges (Chandler, 1961, p. 151). The Virginia specimen is distinct from other fossil species of *Tinospora* in having a dorsal ornamentation of ridges rather than spines or tubercles. This comparison is tempered by the observation that the dorsal surface of *T. elongata* Manchester (Manchester, 1994) is unknown, although the latter still is more elongate than the Virginia fossil. In light of its distinctive characters, the Virginia specimen is recognized as a new species.

#### Family Nyssaceae Genus *Nyssa* L.

The living genus encompasses six species of deciduous trees. Three occur in eastern North America extending into eastern Mexico. A fourth occurs in Panama, a fifth in China and the last in Indomalaysia (Eyde, 1963; Hammel and Zamora, 1990). The endocarps are distinctive in being thick-walled, possessing a ridged exterior, and germinating by means of a triangular germination valve. They are commonly one locular, but occasionally display a second, often reduced, locule (Eyde, 1963), and *N. talamancana* (Hammel and Zamora, 1990) possesses two to three locules.

The fruits of *Nyssa* have an extensive fossil record. The genus is represented by three species in the early Eocene London Clay (Reid and Chandler, 1933; Chandler, 1961: *Paleonyssa multilocularis* Reid and Chandler should be included in *Nyssa*, as its sole distinction is its multilocular condition, a feature now observed in the living *N. talamancana*). In western North America, three species are present in the middle Eocene Clarno Nut Beds flora

(Manchester, 1994), at least one and possibly two species are in the late Eocene Auriferous Gravels flora of the Northern Sierra (Tiffney, personal data). Other species are present in later Tertiary deposits of North America (Tiffney, 1994b, personal data) and Europe (Kirchheimer, 1957; Eyde and Barghoorn, 1963).

#### *Nyssa* species Plate Two, Figures 3, 4, 5.

**Material:** Three endocarps, two smaller and broken, the third larger and exhibiting a clear germination valve. All three preserved as original organic material infiltrated by pyrite. The endocarps are assigned USNM #495849, 495850 and #495851, and were collected by Mr. Thomas Parks and Mr. Michael Folmer.

**Description:** The largest specimen is 14.8 mm long by 7.0 mm wide. The nearly complete small specimen is 10.2 mm long by 4.6 mm wide; the incomplete small specimen is 7.2 mm long and 4.6 mm wide. All three endocarps are elongate, with parallel lateral margins and broadly rounded apices and bases; all are slightly flattened in the dorso-ventral plane. All three are traversed by eight low, rounded ridges running from the apex to the base of the endocarp. The largest endocarp has a clear germination valve about 3/4 the length of the face; a matching valve is not visible on the opposite side, although this may be a function of the distortion of this face. Both smaller specimens were broken on receipt, and the germination valves were not apparent. However, in one case this allowed recognition of two locules within the endocarp.

**Discussion:** The overall shape and the ridged surface of the endocarps, together with the distinctive nature of the spatulate germination valve, serve to ally these fossils with *Nyssa*. The combination of two locules and their small size distinguishes the Virginia fossils from species previously described from the London Clay flora or the Clarno Nut Beds flora. Their greatest similarity among Eocene species lies with specimens from the late Eocene Auriferous Gravels flora of California (Tiffney, unpublished data), which are of a similar size and morphology. The limited number of specimens and their condition leads me to refrain from assigning a species name at this time. It is possible that the largest of the three specimens was genetically distinct from the other two, and that two species of *Nyssa* are present in the flora, a not uncommon occurrence.

#### Family Symplocaceae Genus *Symplocos* Jacq.

The living genus consists of 250 (Nooteboom, 1975; Mabberley, 1987) to 350 (Willis, 1973) species of small evergreen shrubs to, less commonly, large trees. Only one species is deciduous. It is divided into two subgenera. Subgenus *Symplocos* (about 100 species) is largely New

World, while subgenus *Hopea* is predominantly Old World (Nooteboom, 1975, 1977). The genus is dominantly tropical and subtropical, with species from the lowlands to montane rainforests (Nooteboom, 1977). One species, *S. tinctoria* (L.) L'Herit. extends to Delaware on the east coast of North America (Fernald, 1970) and three species extend south to Paraguay (personal herbarium data). Of potential note, all of the New World species that I have examined, and that are reviewed by Mai (1986), possess relatively smooth fruit surfaces. At present, literature and herbarium studies suggest that endocarps with pronounced wings (e.g., *S. costata* (Bl.) Choisy, *S. cerasifolia* Wall. ex DC, *S. barringtoniifolia* Brand.; see Nooteboom, 1975) occur only in the Old World.

*Symplocos* is a common constituent of Eocene through Miocene floras of the Northern Hemisphere. Over 20 species have been described from Europe (Mai, 1970); in some cases individual species are represented by large numbers of specimens in a single deposit (Nooteboom, 1975, 1977). It is known in North America from the middle Eocene Clarno Nut Beds flora (Manchester, 1994), the late Eocene Auriferous Gravels flora of California (Tiffney unpublished data), and the early Miocene Brandon Lignite (Tiffney, 1994b). Three species with large ridges are known from the Miocene of Europe (Mai, 1970) and one (possibly two) species are known from the late Eocene Auriferous Gravels flora of Northern California (Tiffney, unpublished data).

*Symplocos grimsleyi* sp. nov.

Plate Two, Figures 6, 7, 8.

**Material:** Six entire endocarps (one sectioned) and a portion of a seventh, preserved as original organic matter. The type specimen is assigned USNM #495852 and was collected by Mr. Gary Grimsley. The remaining specimens are assigned USNM #495853 through #495858 and were collected by Mr. Gary Grimsley and Mr. Michael Folmer.

**Derivation of name:** The specific name honors Mr. Gary Grimsley of the Maryland Geological Society, who collected and made available for study several specimens from the Fisher/Sullivan site, and who provided assistance in electronic communication between author and editor.

**Description:** The endocarps average 10.2 mm long ( $N=6$ ; maximum 11.2 mm, minimum 8.9 mm) and 5.2 mm in widest diameter ( $N=6$ ; widest 7.1 mm, narrowest 3.8 mm), possessing a 2:1 length to width ratio. The endocarps are elongate, tapering towards both ends. The basal (attachment) end is truncated by a pit which contains three pores, leading to the locules within. The outer surface of the endocarp is marked by 10 equally-spaced, high, thin flanges. These possess undulate crests, perhaps in part a function of preservation. In the sectioned specimen, the endocarp contains three locules surrounding a thin central cavity. Two of the three locules contain remnants of a seed possessing a thin black seed coat. The third is empty and

presumed abortive. The outer endocarp wall consists of radially-elongate sclereids that possess a reflectivity suggestive of a high lignin content. Each of the locules is surrounded by circumferentially-elongate sclereids of a lighter brown color and a more loosely-packed appearance.

**Discussion:** The truncating basal depression represents the juncture of the fruit to the subtending axis. The piercing of this depression by pores leading to three to five individual locules surrounding a central cavity is distinctive of the genus *Symplocos*. Beyond these characters, the fruits of the modern species exhibit a range of sizes, shapes and surficial morphologies. The Virginian endocarp is most similar to several living Old World species of *Symplocos* that possess highly ridged endocarps. Among existing fossils, the Virginia specimens are most similar to *S. schereri* Kirchheimer (Kirchheimer, 1936; Mai, 1970); both possess robust flanges and a fairly thick fruit wall and are of approximately the same size. However, there are about 13 flanges on *S. schereri*, and they tend to be of varying heights and widths, while there are 10 flanges on the Virginia specimens. The *Symplocos* from the Auriferous Gravels flora of Northern California (Tiffney, unpublished data) are also similar, but possess up to 16 slightly lower ridges.

#### Family Vitaceae

Seeds of the Vitaceae are easily recognized by the circular dorsal chalaza and paired ventral infolds flanking the path of the raphe. Variation in the placement of the chalaza, the strength of the raphe, the width and depth of the ventral infolds, the sculpting of the seed surface, and cellular structure of the wall appear to allow identification to genus (Tiffney and Barghoorn, 1976; Latiff, 1994, Manchester, 1994), although it is clear that some characters intergrade between genera (Manchester, 1994). Generic identifications are thus more probabilities than certainties within the family, especially in the absence of large samples amenable to statistical analysis. The descriptive terminology used here is from Tiffney and Barghoorn, 1976, figure 1, except that the terms base and apex are reversed from that figure, which was in error.

The Vitaceae are common components of the Early Tertiary floras of the Northern Hemisphere, and are often represented by substantial numbers of specimens and species in a given deposit. By example, Chandler (1961) recognized 21 species in five genera from the London Clay, Tiffney and Barghoorn (1976) recognized four species in two genera from the Brandon Lignite, and Manchester (1994) recognized seven species in four genera from the Clarno Nut Beds flora. Thus, it is not unexpected that the three specimens so far recovered from the Fisher/Sullivan flora represent two and possibly three separate morphologies.

### Genus *Vitis* L.

In the present day, *Vitis* includes about 60-70 (Willis, 1973; Mabberley, 1987) species of vines distributed in the Northern Hemisphere. The majority of these are warm-temperate to subtropical in distribution, but several species extend to cold-temperate environs. This wide ecological amplitude limits the utility of *Vitis* seeds for paleoclimatic interpretation. However, the presence of the genus is consistent with a warm, frost-free environment. Within the genus *Vitis*, there is considerable variation. It is possible to categorize variation and recognize distinct morphological (and presumably genetic) groupings within a deposit, but I am increasingly convinced (contra Tiffney and Barghoorn, 1976) that comparisons between fossils from different localities, or between fossil and living species, are generally unwarranted.

*Vitis* species #1  
Plate Two, Figures 9, 10.

**Material:** One seed, original organic material with pyrite. This is assigned USNM specimen #495859, and was collected by Mr. Michael Folmer.

**Description:** Seed 7.3 mm long and 4.9 mm wide, strongly flattened in the dorso-ventral plane. The ventral infolds are narrow and parallel, 4.2 mm in length. The dorsal face has been eroded, but possesses an elongate chalazal knot about 2.0 mm long by 0.8 mm wide. A dorsal groove runs from the apex to the base of the seed, but the basal portion has been broken off, making it impossible to judge how deep the groove around the base of the seed was. The raphe is eroded. The seed wall is composed of a layer of radially elongate sclereids.

**Discussion:** The parallel, narrow, ventral infolds and pronounced chalaza to apex and chalaza to base groove suggest this seed belongs to *Vitis*, although the lack of the base of the seed is vexing. The general conformation of the seed, its squared outline, and the elongate infolds are similar to *V. magnasperma* Chandler (Chandler, 1961) of the London Clay flora, which is also present in the Clarno Nut Beds flora (Manchester, 1994), although the Virginia specimen lacks ruminations radiating from the chalaza.

*Vitis* species #2  
Plate Two, Figures 11, 12.

**Material:** One seed, pyritized. This is assigned USNM specimen #495860, and was collected by Mr. Michael Folmer.

**Description:** Seed 4.8 mm long, 3.8 mm wide and 2.8 mm deep (dorsal to ventral face), the apex with a pronounced beak. The ventral infolds are parallel, 1.3 to 1.5 mm in length, moderate in width. The dorsal surface is flattened and bears a central, raised, chalazal knot, occupying 1/3 to 1/2 the dorsal face. There is a weak chalaza to apex groove. A chalaza to base groove is not apparent; the raphe runs from the chalaza around the base on the surface of the seed,

creating a positive ridge. The surface of the seed is smooth, lacking any sign of radial striations. The seed wall is composed of elongate sclereids.

**Discussion:** This seed is most similar to those of *Vitis* in possessing parallel ventral infolds, a chalaza to apex groove and an elongate hilar beak. However, the chalaza to base groove is absent, a situation seen in seeds of *Ampelopsis*. The assignment is made to *Vitis* on the preponderance of characters and its general similarity to species from the London Clay (Chandler, 1961) and Brandon Lignite (Tiffney and Barghoorn, 1976).

### Genus *Ampelopsis* Michx.

*Ampelopsis* is a genus of Atlantic North American and subtropical East Asian deciduous vines. While Willis (1973) and Mabberley (1987) claim the genus has two species, other sources (Melchior, 1964; Bailey, 1928) state 20 species are present. It is known in the fossil record from the London Clay flora (Reid and Chandler, 1933; Chandler 1961) and the Clarno Nut Beds flora (Manchester, 1994).

*Ampelopsis* species  
Plate Two, Figures 13, 14.

**Material:** One seed, preserved largely as original organic matter. This is assigned USNM specimen #495861, and was collected by Mr. Gary Grimsley.

**Description:** Seed relatively undistorted, spherical, 4.7 mm long, 3.8 mm wide and 3.6 mm deep (dorsal to ventral face). The apex has a mildly pronounced beak. The ventral infolds are divergent, 2.5 mm in length. The dorsal surface is strongly arched and bears a central, low, chalazal knot, about 1.0 mm in diameter. There is no groove on the dorsal face. The raphe runs from the chalaza around the base on the surface of the seed, creating a positive ridge. The entire surface of the seed is marked by elongate radial striations.

**Discussion:** The absence of a groove on the dorsal face and the resulting positive topography of the raphe around the basal end, together with the round shape, radiate markings of the seed surface and the divergent infolds, suggest that this seed represents *Ampelopsis*. The fossil is also similar to seeds of *Cayratia* Juss., but in the latter genus the chalazal knot is very large and elongate, and the seed has a prominent beak (Latiff, 1994). Similar seed morphology also is observed in *Parthenocissus* Planch.; however, here the seed surface tends to be smooth and the ventral folds are parallel.

### Unknowns

Unknown angiosperm #1  
Plate Three, Figures 1, 2.

**Material:** Two seeds, both heavily pyritized, one broken on the ventral surface. These are assigned USNM specimen #495862 and 495863, and were collected by Mr. Michael Folmer.

**Description:** The larger seed is 6.6 mm long and 4.7 mm broad, the smaller (broken) is 6.2 mm long and 4.2 mm broad; both are elliptic to broadly elliptic in face view. In cross section, they possess a convex dorsal face and two flat ventral faces which meet on the ventral midline in a sharp angle, suggesting that several seeds were arranged around a common axis within the fruit. An apparent zone of weakness is present at the apex of the ventral angle, as both seeds have split along this lineation. The margins of this zone of splitting appear slightly thicker than the adjacent seed wall. Both the dorsal and ventral surfaces are covered by a pattern of low bumps that frequently coalesce to form a low rumpled pattern of ridges. At higher magnification, the entire surface is covered with very fine, even pitting, perhaps reflecting the outer layer of cells of the seed. The broken specimen reveals the seed wall to be two layered. The outer layer is formed of one layer of radially elongate sclereids which occupy about 2/3 the width of the seed coat. The inner layer is indistinct, but clearly of a different structure. The interpretation that these are seeds and not cocci of a fruit is based upon the absence of any clear evidence for a second internal structure within the broken specimen. A possible argument against this interpretation is the fact that these fossils possess no clear sign of a hilum or micropyle.

**Discussion:** This fossil is outwardly somewhat similar to *Carpolithus bellispermus* Chandler (Chandler, 1978) in overall shape and the tubercular surface. However, *C. bellispermus* is half the size of the Virginia specimens, and possesses a large hilar scar.

Unknown Angiosperm # 2.  
Plate Three, Figures 3, 4, 5, 6.

**Material:** Two fruits, one intact, one broken; both pyritized. These are assigned specimen #495864 and #495865. One was collected by Mr. Michael Folmer and one by Mr. Gary Grimsley.

**Description:** Fruit a compressed oblong sphere, the entire specimen 7.1 mm long and 5.3 mm by 4.3 mm in diameter, the broken one 6.6 mm high and 5.7 mm by 3.9 mm in diameter. It is unclear if the diameter differences are original or preservational. The fruit is surrounded by eight fairly evenly-spaced low longitudinal ridges. Two ridges on opposing faces possess a distinct groove atop the ridge. This groove meets at the top and bottom of the fruit, suggesting that it represents the plane of separation between two carpels. The apices of the grooved ridges are marked by fine horizontal striations that are not apparent on the remaining six ridges. The apex of the fruit is capped by a short, bilobed, mound, suggestive of a stigma and/or style. The base possesses a small pit, suggestive of a point of attachment. The broken specimen reveals a single central cavity, suggesting the fruit was unilocular at maturity. No details of the cellular structure of the wall could be ascertained.

**Discussion:** There is some similarity to *Carpolithus* species

1 of the Clarno Nut Beds flora (Manchester, 1994, plate 66, figures 11-14), but the latter fruit possesses grooves at the apex of each of its longitudinal ribs, and lacks the apparent stigmatic crest of the Virginia specimen.

Unknown object #1  
Plate Three, Figure 7.

Sphere, 5.4 mm in diameter, sitting upon a small stalk about 2.0 mm in length, the entire object of pyrite. The stalk melds directly into the sphere. There is no surficial cellular detail apparent. Assigned USNM #495866, collected by Mr. Michael Folmer.

This object initially was taken to be a fruit of the Lauraceae sitting within its cupule. Careful examination revealed that the sphere and stalk are continuous, the apparent seam being formed by a circumferential break in the layer of pyrites. This may simply be a concretion.

Unknown object # 2  
Plate Three, Figure 8.

Hollow lenticel, 32 mm long, 17.6 mm wide and 6.3 mm thick. The external detail is obscured by sediment in a pyrite cement. The wall appears made of elongate cells oriented in the direction of the long axis of the structure. The central portion of the structure is hollow and contains a small amount of material of an apparently different cellular makeup; however, the structure is very unclear. Assigned USNM # 495867; collected by Mr. Michael Folmer.

This object is most likely a worn, flattened piece of wood. However, the apparent difference between the surface and the "contents" of the structure warrant its description.

### Family Palmae Genus *Nypa* Steck

*Nypa* is a monotypic genus of palms that grows in brackish water environments, often forming a backswamp community behind the mangroves of the immediate coastline (Tralau, 1964; Collinson, 1993). It possesses large, distinctive fruits, borne in terminal clusters. Each pear-shaped fruit is composed of an outer longitudinally fibrous sheath, enclosing a hard endocarp within which is the seed. Dispersal is by water, and individual fruits can float for long periods of time.

*Nypa* is a very common fossil in the Eocene sediments of Europe (Tralau, 1964; Collinson, 1993), and is also known from the Eocene of Egypt (Gregor and Hagn, 1982; Tiffney, unpublished data) and the Eocene of Texas (Tralau, 1964; Gee, 1990).

The fossil fruit reported here does not come from the Fisher/Sullivan site, but from the Woodstock member of the Nanjemoy Formation at Popes Creek, Maryland, in association with *Wetherellia* (Mazer and Tiffney, 1982). The Woodstock member lies above the Potapaco Member of the Nanjemoy Formation, and bridges the calcareous

nannofossil zones NP 13 and NP 14, indicating an age of about 53.5 to 52 Ma (Gibson and Bybell, 1991; Weems and Grimsley, this volume), about three million years younger than the rest of the fossils reported here. It is included in this report as it clearly is part of the same regional vegetation of the early Eocene.

*Nypa* cf. *burtini* (Brongniart) Ettingshausen  
Plate Three, Figure 9, 10.

**Material:** One endocarp, originally preserved as a thin shell of fibrous organic matter in a greensand matrix. Despite efforts at conservation, the specimen self-destructed within months of receipt, and all that remains is the photographic record. The specimen was collected by Mr. Robert Wiest.

**Description:** Endocarp 8.0 cm wide and 6.9 cm long. The basal portion of the endocarp is missing; judging from the curve of the endocarp and from living specimens, the endocarp was probably about 10 cm long. The actual fruit (including the fibrous exocarp) was probably larger. The endocarp surface is marked by fine longitudinal striations, presumably reflecting the adjacent fibers of the exocarp. The endocarp wall is 1–2 mm thick, and the locule is infilled by sediment.

**Discussion:** The size, shape and striated surface of this fossil are very similar to the endocarps of living *Nypa*. However, while I have had this fossil for 15 years (courtesy of Mr. Robert Wiest), I had never observed a similar mode of preservation, and awaited further specimens to validate the identification. The discovery of the Fisher/Sullivan flora with its clear association with the London Clay flora provides circumstantial support for the identification. Further, in 1996, Dr. Margaret Collinson examined this fossil and informed me that *Nypa* was known in Europe in this style of preservation (cf., Collinson, 1993). Since this fossil adds to the larger picture of the Ypresian flora of Atlantic North America, I have included its description here. Its presence underscores the similarity of the depositional environments of the London Clay flora (Collinson, 1993) and the flora from the Fisher/Sullivan site.

It is possible that this is not the first report of *Nypa* from Virginia. Berry (1936) described *Ficus aquiana* from the Paleocene Aquia Formation, immediately underlying the Nanjemoy. Examination of his illustration (1936, figure 2) and text suggest that the object, if inverted from his illustration, would conform well to the endocarp of *Nypa*. The length to breadth and breadth to thickness ratios of this fossil agree with similar measurements for small *Nypa* fruits from living plants and from the European Eocene (Collinson, 1993). It is also possible that this object is neither *Nypa* nor *Ficus*; this speculation can only be resolved by examining the actual specimen (NMNH catalog #P 039367).

## DISCUSSION

The small size of the flora from the Fisher/Sullivan site notwithstanding (ten identified taxa and two unidentified),

its composition allows some interesting insights into the vegetation, climate and paleobiogeographic affinities of Virginia during the early Eocene. The occurrence of *Nypa* in nearly coeval sediments of the same formation in adjacent Maryland adds further to this picture.

It might be tempting to compare these insights with inferences from fossils from the immediately underlying Paleocene Aquia Formation, where E. W. Berry reported the presence of both a fig (Berry, 1936) and a pine cone (Berry, 1934), using these to argue for a temperate Paleocene climate. Even if correctly identified, both genera possess species that live in subtropical environments. However, these identifications require verification; as noted above, the “fig” could be a *Nypa* endocarp. In light of these uncertainties, no such comparisons will be made.

**Vegetation.** We may estimate the habit of the parent plant of a fossil fruit or seed from the habit of its nearest living relatives. In the Fisher/Sullivan flora, this is possible for eight genera. Of these, two are trees, one is a shrub, one is a palm, and four (*Ampelopsis*, *Iodes*, *Tinospora* and *Vitis*) are vines. This pattern of a large proportion of vines is also seen in the Clarno Nut Beds flora, where 43 percent of the taxa for which habit could be inferred were climbers, and the London Clay flora, where vines and lianes are extraordinarily common (Reid and Chandler, 1933; Chandler, 1961; Collinson, 1983). Vines and lianes are very common in tropical rain forests, forming between eight percent (Richards, 1952) and 28 percent (Gentry, 1992) of the species diversity. By contrast, they are far less common in temperate communities (Richards, 1952). The dominance of large vines or lianes thus suggests that the forest of the Virginian Eocene coastal plain was similar in structure to modern tropical or paratropical forests, with a multi-layered canopy and a deeply shaded forest floor (Richards, 1952). While vine diversity suggests that the Fisher/Sullivan, Clarno Nut Beds and London Clay Floras were possessed of a tropical vegetation, vines appear over-represented in these floras by modern standards. This could reflect their actual Eocene diversity as suggested by Crane (1987), but it is also possible that a bias towards their preservation is at work. Vines and lianes often possess relatively large seeds, and frequent areas of higher light intensity, including stream margins (Richards, 1952). These features might favor their disproportionate fossilization and discovery in these Eocene floras.

Of the eight genera for which nearest living relatives may be identified, four are evergreen (*Canarium*, *Iodes*, *Nypa* and *Tinospora*), two have both evergreen and deciduous species (*Vitis* and *Symplocos*, although deciduous species are very rare in the latter genus) and two are deciduous (*Ampelopsis* and *Nyssa*). The intermixture of deciduous and evergreen elements is a common pattern in Early Tertiary floras of the Northern Hemisphere (Reid and Chandler, 1933; Manchester, 1994). While it is possible that it represents the taphonomic intermixing of remains from different source communities (e.g., Gray, 1960), it appears more likely that it represents a

vegetation for which there is no living equivalent. In such vegetation, evergreen taxa dominate, but with an admixture of deciduous elements, the latter perhaps occupying sites governed by edaphic factors (Wolfe, 1975, 1985).

From the perspective of the geographic occurrence of the nearest living relatives, four of the genera (*Ampelopsis*, *Nyssa*, *Symplocos* and *Vitis*) live in Virginia today. *Symplocos*, however, is represented by only one species; the vast majority of its species are subtropical to tropical. Four of the genera (*Canarium*, *Iodes*, *Nypa* and *Tinospora*) are found in the Old World tropics, predominantly in southeastern Asia. The flora from the Fisher/Sullivan site thus parallels the pattern observed in other Paleogene and early Miocene floras of Europe and North America, where the predominant number of nearest living relatives survive in southeast Asia (Tiffney, 1985a, 1985b, 1994a).

**Climate.** Optimally, one would like to estimate paleoclimate by a method that is independent of the identification of the individual fossils, such as is possible with the characters of leaves (Wolfe, 1993). Unfortunately, in present understanding, fossil fruits and seeds do not possess such characters, and the estimation of the paleoclimate is through analogy to the environments of growth of the nearest living relatives. This method has inherent pitfalls, including the difficulty posed by misidentifications and the possibility that genera have changed their climatic tolerances over evolutionary time (Manchester, 1994; Tiffney, 1994a). The ranges of living species of *Ampelopsis*, *Nyssa*, *Symplocos* and *Vitis* all extend to areas of the Northern Hemisphere that experience extended periods of freezing temperatures in winter (e.g., Fernald, 1970). However, in all cases, other species of the genus live in frost-free paratropical, or in some cases, full-tropical, climates. By contrast, modern species of *Canarium* (Leenhouts, 1959), *Iodes* (Sleumer, 1971; Villiers, 1973), *Tinospora* (Forman, 1981) and *Nypa* (Collinson, 1993) inhabit entirely frost-free paratropical or full-tropical climates in the present day. Given that these genera existed together in the Fisher/Sullivan flora, one is faced with two hypotheses; either the paleoclimate approximated that of the present day, and some taxa have evolved to tolerate warmer climates, or the paleoclimate was warmer than the present day, and some taxa have evolved to tolerate cooler climates.

Nonbotanical estimators of paleoclimate demonstrate that the Early Tertiary was a period of warmth, with frost-free climates to high latitudes (e.g., Miller, Fairbanks and Mountain, 1987; Spicer and Chapman, 1990; Sloan and Barron, 1992). At approximately the Eocene - Oligocene boundary the climate rapidly cooled (Kennett, 1977) leading to a gradual decline in global temperatures culminating in the polar glaciations of the Pleistocene. Given this pattern, it is more parsimonious to assume that the Fisher/Sullivan biota grew under a paleoclimatic regime that resembles that of the most frost-intolerant of the nearest living relatives, rather than that of the most frost-tolerant ones. Tiffney (1994a) describes

a graphic method of estimating paleoclimates from nearest living relative data by superimposing a plot of the geographic range of all the taxa involved in a given flora and then identifying the place or places where the largest number of taxa co-occur in the present day. Climatic data are sought out for weather stations occurring in the areas of high co-occurrence, particularly those at the coolest localities in order not to over-estimate the temperature. This methodology is crude and provides only an approximation of the paleoclimate. Further, the validity of this approach improves with the size of the sample, and eight species is a small sample. With these cautions, this approach suggests that the paleoclimate at the Fisher/Sullivan site was perhaps equivalent to that of southern China in the area of Canton and Hainan island. Taking climatic records from Wuchow and Nanning in this area (Tiffney, 1994a), suggests a mean annual temperature of about 22.5°C, a mean annual range of about 16°C, and coolest month mean temperatures well above freezing. The same method probably is not an accurate indicator of absolute amounts of precipitation, as what is really significant is the evapotranspiration potential which is a function of both ambient temperature and water availability. However, this method suggests that rainfall was adequate on a year round basis, without extended periods of water stress.

**Paleogeography.** The Fisher/Sullivan flora fulfills the prediction of the hypothesis that the North Atlantic was an important route of biogeographic exchange between western Europe and North America in the Early Tertiary. All nine of the identified genera from the Fisher/Sullivan flora (if one accepts *Tricarpellites communis* as a species of *Canarium*), together with the nearly coeval *Nypa* from the Popes Creek locality, occur in the London Clay flora. Further, two of these taxa, *Nypa* and *Wetherellia*, are amongst the most common fossils in the London Clay. The strength of this particular biogeographic link is further reinforced by the similarity of the fish fauna between the Nanjemoy Formation and the London Clay (Weems and Horman, 1983; Weems and Grimsley, this volume).

Six of the taxa from the Fisher/Sullivan flora also occur in the Clarno Nut Beds. In truth, the latter figure is misleading, as *Nypa* is a mangrove and *Wetherellia* is assumed to be a mangrove, both thus requiring salt water which is absent at the inland Nut Beds site.

In sum, the flora from the Fisher/Sullivan site strongly suggests that the Early Tertiary North Atlantic provided an important route of floristic exchange between the New and Old Worlds. This is not surprising given the concatenation of events that occurred in the Early Tertiary. The peak in global warmth coincided with a period of rapid evolutionary radiation in angiosperms, mammals and possibly birds (Tiffney, 1984). The North Atlantic Land bridge provided a route for intercontinental exchange, resulting in an early Eocene peak in mammalian generic similarity between Europe and North America (Lehmann, 1973). The evolving vertebrates presumably established dispersal relationships

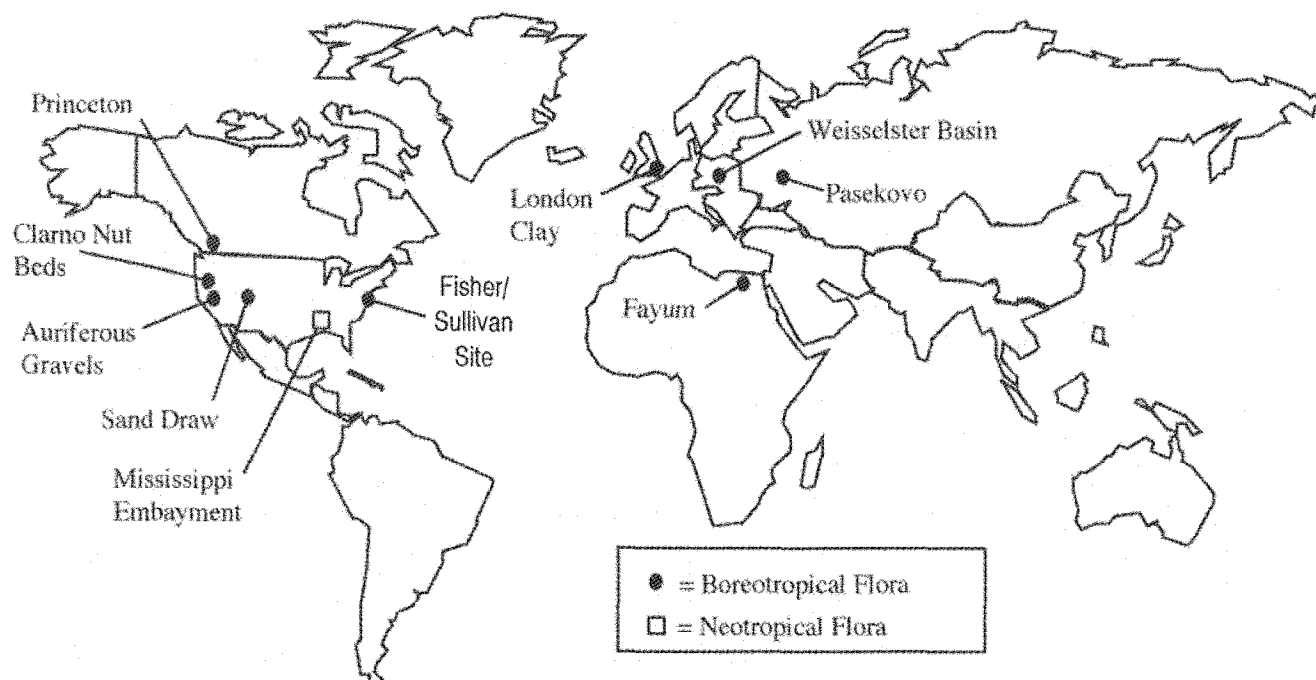


Figure 1. Geographic distribution of some of the fossil floral localities mentioned in the text as dominated by the Boreotropical Flora during the Eocene. References are in the text.

with angiosperms (Tiffney, 1984; Collinson and Hooker, 1991). Thus, it is not surprising that the same route that allowed vertebrate exchange would also allow the spread of newly evolved angiosperms (Figure 1). In addition, the warm climate and the relatively narrow North Atlantic of the early Eocene would favor the spread of mangrove plants along the coastlines via water dispersal.

While the evidence that the Fisher/Sullivan flora provides for the route of spread of the Boreotropical Flora is compelling, it is outweighed by the promise of the future. The London Clay flora is one of the most diverse fruit and seed floras known from the Early Tertiary, in part because its marine setting allows a sample of both coastal vegetation, and the vegetation of inland areas, transported to sea by rivers. It is to be hoped that further collecting from the Nanjemoy Formation will yield an equally diverse flora in time, although the amount of exposure in Virginia may be less than that in the London Clay.

#### ACKNOWLEDGMENTS

I am grateful to The Maryland Geological Society and its members Mark Bennett, Michael Folmer, Gary Grimsley, Ron Keil, Thomas Parks and others I may not be aware of who have made their finds available for description. Mr. Dennis Fisher, Mr. Larry Fisher, and Mr. Russell Sullivan kindly made their property available for collectors. I thank Mr. Robert Wiest for his courtesy in sending me the *Nypa* fruit from Popes Creek, Maryland. I thank Dr. Robert Weems for organizing these collections and sending me material. Dr. Steven Manchester (University of Florida Museum of Natural History) has offered constructive criticism and advice, which is gratefully acknowledged.

#### BIBLIOGRAPHY

- Allison, P. A., 1988, Taphonomy of the Eocene London Clay biota: *Palaeontology*, v. 31, part 4, p. 1079-1100.
- Bailey, L. H., 1928, *The Standard Cyclopedia of Horticulture*, Second Edition, v. 1: (Macmillan Co., New York), xxiv. + 1200 pp.
- Berry, E. W., 1934, A pine from the Potomac Eocene: *Journal of the Washington Academy of Sciences*, v. 24, p. 182-183.
- Berry, E. W., 1936, A fig from the Eocene of Virginia: *Journal of the Washington Academy of Sciences*, v. 26, p. 108-111.
- Call, V. B., Manchester, S. R., and Dilcher, D. L., 1993, *Wetherellia* fruits and associated fossil plant remains from the Paleocene/Eocene Tuscaloosa-Hatchetigbee interval, Meridian, Mississippi: *Mississippi Geology*, v. 14, number 1, p. 10-18.
- Chandler, M. E. J., 1954, Some Upper Cretaceous and Eocene fruits from Egypt: *Bulletin of the British Museum (Natural History)*, v. 2, number 4, p. 149-187.
- Chandler, M. E. J., 1961, The Lower Tertiary Floras of Southern England. I. Palaeocene Floras; London Clay (Supplement): (British Museum of Natural History, London) xi + 354 pp.
- Chandler, M. E. J., 1962, The Lower Tertiary Floras of Southern England. II. Flora of the Pipe-clay series of Dorset (Lower Bagshot): (British Museum of Natural History, London) xi + 176 pp.
- Chandler, M. E. J., 1964, The Lower Tertiary Floras of Southern England. IV. A summary and survey of findings in the light of recent botanical observations: (British Museum of Natural History, London) xii + 151 pp.
- Chandler, M. E. J., 1978, Supplement to the Lower Tertiary Floras of

- southern England, part 5: Tertiary Research Special Paper Number 4, p. 1-47.
- Collinson, M. E., 1983, Fossil Plants of the London Clay, The Palaeontological Association Field Guide to Fossils, number 1, p. 1-121.
- Collinson, M. E., 1993, Taphonomy and fruiting biology of recent and fossil *Nypa*: The Palaeontological Association, Special Papers in Palaeontology, number 49, p. 165-180.
- Collinson, M. E., and Hooker, J. J., 1991, Fossil evidence of interactions between plants and plant-eating mammals: Philosophical Transactions of the Royal Society, London, v. 333, p. 197-208.
- Crane, P. R., 1987, Vegetational consequences of angiosperm diversification: p. 107-144 in, E. M. Friis, W. G. Chaloner, and P. R. Crane, eds., The Origins of Angiosperms and their Biological Consequences, (Cambridge University Press, Cambridge).
- Dilcher, D. L., 1973, A revision of the Eocene floras of southeastern North America: Palaeobotanist, v. 20, p. 7-18.
- Erwin, D. M., and Stockey, D. A., 1994, Permineralized monocotyledons from the middle Eocene Princeton Chert (Allenby Formation) of British Columbia, Canada: Arecaceae: Palaeontographica Abteilung B., Paläophytologie, v. 234, p. 19-40.
- Eyde, R. H., 1963, Morphological and paleobotanical studies of the Nyssaceae, I. A survey of the modern species and their fruits: Journal of the Arnold Arboretum, v. 44, p. 1-54.
- Eyde, R. H., and Barghoorn, E. S., 1963, Morphological and paleobotanical studies of the Nyssaceae, II. The fossil record: Journal of the Arnold Arboretum, v. 44, p. 328-370.
- Fernald, M. L., 1970, Gray's Manual of Botany, Eighth edition: (Van Nostrand Reinhold, New York) lxiv + 1632 pp.
- Forman, L. L., 1981, A revision of *Tinospora* (Menispermaceae) in Asia to Australia and the Pacific. The Menispermaceae of Malesia and adjacent areas: XI: Kew Bulletin, v. 36, number 2, p. 375-421.
- Forman, L. L., 1986, Menispermaceae. in: Flora Malesiana, Series 1, v. 10, number 2, p. 209-296.
- Frederiksen, N. O., 1995, Differing Eocene floral histories in southeastern North America and western Europe: Influence of paleogeography: Historical Biology, v. 10, p. 13-23.
- Gee, C. T., 1990, On the fossil occurrences of the mangrove palm *Nypa*: p. 315-319 in, E. Knobloch and Z. Kvacek, eds., Proceedings of the Symposium Paleofloristic and Paleoclimatic Changes in the Cretaceous and Tertiary (Czech Geological Survey, Prague).
- Gentry, A. H., 1992, The distribution and evolution of climbing plants: p. 3-43 in, F. E. Putz and H. A. Mooney, eds., The Biology of Vines (Cambridge University Press, Cambridge).
- Gibson, T. G., and Bybell, L. M., 1991, Paleocene-Eocene sedimentation in the Potomac River Valley, Virginia and Maryland: IGCP Project 308, Fieldtrip Guidebook, 124 pp.
- Graham, A., 1972, Outline of the origin and historical recognition of floristic affinities between Asia and Eastern North America: p. 1-18 in, A. Graham, ed, Floristics and Paleofloristics of Asia and Eastern North America (Elsevier, Amsterdam).
- Gray, A., 1840, Dr. Siebold, Flora Japonica (Review): American Journal of Science and Arts, v. 39, p. 175-176.
- Gray, A., 1878, Forest geography and archaeology. A lecture delivered before the Harvard University Natural History Society: American Journal of Science and Arts, Series III, v. 16, p. 85-94, 183-196.
- Gray, J., 1960, Temperate pollen genera in the Eocene (Claiborne) flora, Alabama: Science, v. 132, p. 808-810.
- Gregor, H.-J., and Goth, K., 1979, Erster Nachweis der Gattung *Canarium* Stickman 1759 (Burseraceae) im europäischen Alttertiär: Stuttgarter Beiträge zur Naturkunde Serie B (Geologie und Paläontologie), v. 47, p. 1-15.
- Gregor, H.-J., and Hagn, H., 1982, Fossil fructifications from the Cretaceous-Paleocene boundary of SW-Egypt (Danian, Bir Abu Munqar): Tertiary Research, v. 4, p. 121-147.
- Hammel, B. E., and Zamora, N. A., 1990, *Nyssa talamancana* (Cornaceae) an addition to the remnant Laurasian Tertiary flora of southern Central America: Brittonia, v. 43, p. 165-170.
- Harland, W. B., Armstrong, R. L., Cox, A. V., Craig, L. E., Smith, A. G., and Smith, D. G., 1990, A Geologic Time Scale 1989: (Cambridge University Press, Cambridge) xvi + 263 pp.
- Hickey, L. J., 1977, Stratigraphy and Paleobotany of the Golden Valley Formation (Early Tertiary) of western North Dakota: Geological Society of America Memoir, v. 150, p. 1-183.
- Kennett, J. P., 1977, Cenozoic evolution of Antarctic glaciation, the circum-Antarctic Ocean, and their impact on global oceanography: Journal of Geophysical Research, v. 82, p. 3843-3860.
- Kirchheimer, F., 1936, Über die Pflanzenreste in den Begleitschichten der Braunkohle von Dürren: Palaeontologische Zeitschrift, v. 18, number 3/4, p. 213-227.
- Kirchheimer, F., 1957, Die Laubgewächse der Braunkohlenzeit: (Verlag W. Knapp, Halle/Saale) ix + 783 pp.
- Knobloch, E., and Mai, D. H., 1986, Monographie der Früchte und Samen in der Kreide von Mitteleuropa: Rozprawy Ustredniho ustavu geologickeho, v. 47, p. 1-219.
- Lam, H. J., 1932, Beiträge zur morphologie der Burseraceae insbesondere der Canarieae: Annales du Jardin Botanique de Buitenzorg, v. 42, p. 97-226.
- LaMotte, R. S., 1952, Catalog of the Cenozoic plants of North America through 1950: Geological Society of America Memoir, v. 51, 381 pp.
- Latiff, A., 1994, On the seeds of modern and fossil taxa of Vitaceae: Malaysian Applied Biology, v. 22, number 1, p. 97-106.
- Lavin, M., and Luckow, M., 1993, Origins and relationships of tropical North America in the context of the boreotropics hypothesis: American Journal of Botany, v. 80, p. 1-14.
- Leenhouts, P. W., 1956, Burseraceae: Flora Malesiana, Series 1, v. 5, p. 209-296.
- Leenhouts, P. W., 1959, Revision of the Burseraceae of the Malaysian area in the wider sense. Xa. *Canarium* Stickm.: Blumea, v. 9, p. 275-475.
- Lehmann, U., 1973, Zur paläogeographie des Nordatlantiks im Tertiär: Mitteilungen aus dem Geologisch-Paläontologischen Institut

- der Universität Hamburg, v. 42, p. 57-69.
- Mabberley, D. J., 1987, *The Plant Book*: (Cambridge University Press, Cambridge) xii + 706 pp.
- Mai, D. H., 1970, Subtropische Elemente im europäischen Tertiär I: Paläontologische Abhandlungen des Zentralen Geologischen Instituts, v. 3B, p. 441-503.
- Mai, D. H., 1986, Über antillanische Symplocaceae: Feddes Repertorium, v. 97, number 1-2, p. 1-28.
- Mai, D. H., 1993, On the extinct Mastixiaceae (Cornales) in Europe: Geophytology, v. 23, number 1, p. 53-63.
- Mai, D. H., and Walther, H., 1985, Die obereozänen Floren des Weissester-Beckens und seiner Randgebiete: Abhandlungen des Staatlichen Museums für Mineralogie und Geologie zu Dresden, v. 33, p. 1-220.
- Manchester, S. R., 1994, Fruits and seeds of the middle Eocene Nut Beds Flora, Clarno Formation, Oregon: Palaeontographica Americana, v. 58, p. 1-205.
- Manchester, S. R., and Tiffney, B. H., 1993, Fossil Fruits of *Pyrenacantha* and Related Phytoceneae (Icacinaeae) in the Paleogene of North America, Europe and Africa: American Journal of Botany, v. 80, number 6, Supplement, page 91 (abstract).
- Mazer, S. J., and Tiffney, B. H., 1982, Fruits of *Wetherellia* and *Palaeowetherellia* (?Euphorbiaceae) from Eocene sediments in Virginia and Maryland: Brittonia, v. 34, number 3, p. 300-333.
- Melchior, H., 1964, A. Engler's Syllabus der Pflanzenfamilien, II. Band, Angiospermen: (Gebrüder Borntraeger, Berlin), 666 pp.
- Miller, K. G., Fairbanks, R. G., and Mountain, G. S., 1987, Tertiary oxygen isotope synthesis, sea level history, and continental margin erosion: Paleocyanography, v. 2, p. 1-19.
- Myers, J. A., 1990, A Bridgerian age flora from Del Mar, California: Master's Thesis, San Diego State University, 164 pp.
- Nooteboom, H. P., 1975, Revision of the Symplocaceae of the Old World, New Caledonia Excepted: Leiden Botanical Series, v. 1, p. 335.
- Nooteboom, H. P., 1977, Symplocaceae: Flora Malesiana, series I, v. 8, number 2, p. 205-274.
- Reid, E. M., and Chandler, M. E. J., 1933, The London Clay Flora: (British Museum of Natural History, London) viii + 561 pp.
- Richards, P. W., 1952, The Tropical Rain Forest: (Oxford University Press, Oxford) xviii + 450 pp.
- Sleumer, H., 1971, Icacinaceae: Flora Malesiana, series I, v. 7, number 1, pages 67-73.
- Sloan, L. C., and Barron, E. J., 1992, A comparison of Eocene climate model results to quantified paleoclimatic interpretations: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 93, p. 183-202.
- Spicer, R. A., and Chapman, J. L., 1990, Climate change and the evolution of high-latitude terrestrial vegetation and floras: Trends in Ecology and Evolution, v. 5, p. 279-284.
- Tiffney, B. H., 1984, Seed size, dispersal syndromes, and the rise of the angiosperms: evidence and hypothesis: Annals of the Missouri Botanical Garden, v. 71, p. 551-576.
- Tiffney, B. H., 1985a, Perspectives on the origin of the floristic similarity between eastern Asia and eastern North America: Journal of the Arnold Arboretum, v. 66, number 1, p. 73-94.
- Tiffney, B. H., 1985b, The Eocene North Atlantic Land Bridge: Its importance in Tertiary and modern phytogeography of the Northern Hemisphere: Journal of the Arnold Arboretum, v. 66, number 2, p. 243-273.
- Tiffney, B. H., 1994a, An estimate of the Early Tertiary paleoclimate of the southern Arctic: p. 267-295 in, M. C. Boulter and H. C. Fisher, eds., Cenozoic Plants and Climates of the Arctic (Springer Verlag, Berlin).
- Tiffney, B. H., 1994b, Re-evaluation of the age of the Brandon Lignite (Vermont, USA) based on plant megafossils: Review of Palaeobotany and Palynology, v. 82, p. 299-315.
- Tiffney, B. H., 1996, New London Clay-type floras from western North America: Phytogeographic and Paleoclimatic implications: Abstract Volume, Fifth Quadrennial Conference of the International Organisation of Palaeobotany, p. 100.
- Tiffney, B. H., and Barghoorn, E. S., 1976, Fruits and seeds of the Brandon Lignite. I. Vitaceae: Review of Palaeobotany and Palynology, v. 22, p. 169-191.
- Tiffney, B. H., and Haggard, K. K., 1995, Fruits of Mastixioideae (Cornaceae) from the Paleogene of western North America: Review of Palaeobotany and Palynology, v. 92, p. 29-54.
- Tralau, H., 1964, The genus *Nypa* Van Wurmb: Kongelige Svenska Vetenskapsakademiens Handlingar, Fjärde Serien, v. 10, number 1, p. 1-29.
- Vickulin, S. V., 1996, New London Clay-type flora from Middle Russian Upland, European Russia: Abstract Volume, Fifth Quadrennial Conference of the International Organisation of Palaeobotany, p. 106.
- Villiers, J.-F., 1973, Icacinaceae: Flore Du Gabon, v. 20, pages 3-100.
- Ward, L. W., 1985, Stratigraphy and characteristic mollusks of the Pamunkey Group (Lower Tertiary) and the Old Church Formation of the Chesapeake Group -- Virginia Coastal Plain: United States Geological Survey Professional Paper, number 1346, p. 1-78.
- Weems, R. E., and Horman, S. R., 1983, Teleost fish remains (Osteoglossidae, Blochiidae, Scombridae, Tridontidae, Diodontidae) from the Lower Eocene Nanjemoy Formation of Maryland: Proceedings of the Biological Society of Washington, v. 96, number 1, p. 38-49.
- Willis, J. C., 1973, A Dictionary of the Flowering Plants and Ferns, eighth edition, edited by H. K. Airy Shaw: (Cambridge University Press, Cambridge) xxii + 1245 + lxvi pp.
- Wolfe, J. A., 1975, Some aspects of plant geography of the Northern Hemisphere during the Late Cretaceous and Tertiary: Annals of the Missouri Botanical Garden, v. 62, number 2, p. 264-279.
- Wolfe, J. A., 1985, Distribution of major vegetational types during the Tertiary: American Geophysical Union, Geophysical Monograph, number 32, p. 357-375.
- Wolfe, J. A., 1993, A method of obtaining climatic parameters from leaf assemblages: United States Geological Survey Bulletin, number 2040, p. 1-73.

**PLATE 1**

Figures 1, 2. *Canarium parksii* sp. nov.

Figure 1. Lateral view (apex up) displaying two of the three carpels within the receptacle. Faint lines demarcate the juncture of the embayment and pyrene, and the margins of the pyrene valve. X 9. USNM #495826 (type).

Figure 2. Lateral view (apex up) of a single pyrene nested within the embayment of the central axis. The coat of the pyrene is broken, revealing the pyritized seed within. X 13. USNM #495827.

Figures 3, 4. *Beckettia* species

Figure 3. Lateral view (apex up); the two carbonaceous locules flank the central sediment-filled zone. The apex faces upward. X 7. USNM #495840.

Figure 4. Apical view; both locules have a shallow dorsal infold; the apex of the left hand locule has been abraded. The presumed third and missing locule would have been on the upper side of the fruit. X 7. USNM #495840.

Figures 5 - 7. *Wetherellia marylandica* (Hollick) Mazer and Tiffney

Figure 5. Lateral view of a dehiscing fruit, the stigmatic apex uppermost. X 3.5. USNM #495841.

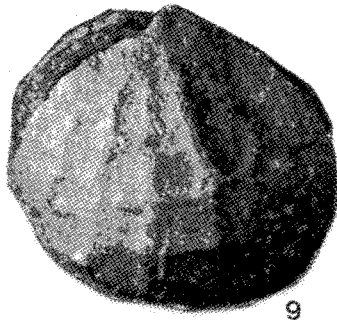
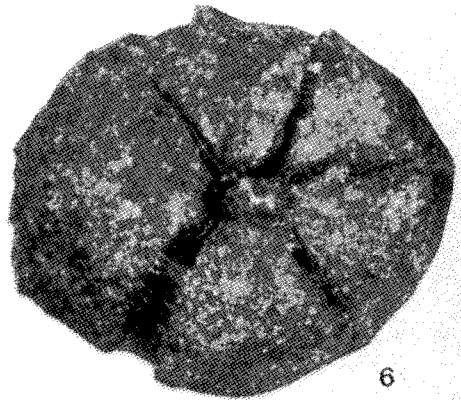
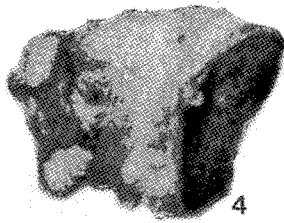
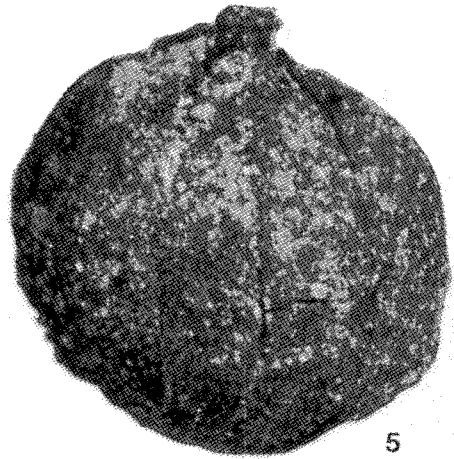
Figure 6. Apical view of same fruit; four of the six cocci have split, the remaining two adhere to one another. X 3.5. USNM #495841.

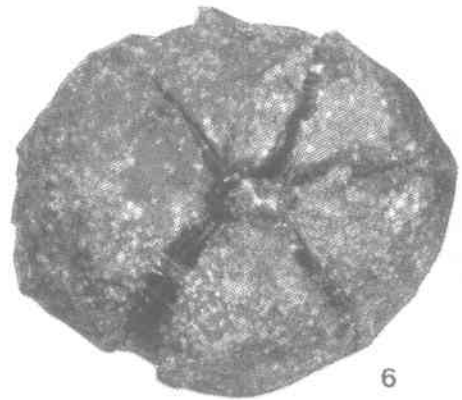
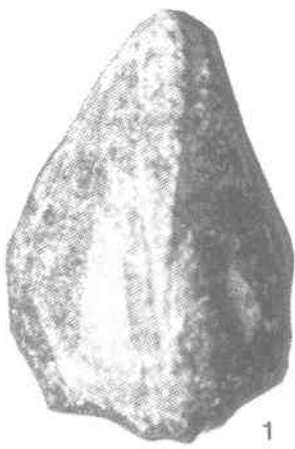
Figure 7. Inner face of a broken carpel, displaying the seed. The raphal trace may be seen as a faint line departing the seed approximately 2/3 of the way up its right margin. X 10. USNM #495842.

Figures 8, 9. *Iodes multireticulata* Reid and Chandler

Figure 8. Carbonaceous endocarp, apex up. Note well-preserved reticulum. X 9. USNM #495846.

Figure 9. Pyritized endocarp, apex up. The reticulum is greatly abraded and the endocarp has begun to split along a longitudinal plane. X 9. USNM #495847.





## PLATE 2

Figures 1, 2. *Tinospora folmerii* sp. nov.

Figure 1. Dorsal view of endocarp. Note medial ridge. The hemispherical surface is traversed by intersecting ridges. X 8. USNM #495848 (type).

Figure 2. Ventral view of endocarp. The ventral depression is filled with reflective pyrites. The dorsal-median ridge curls around each end and disappears into the ventral depression. X 8. USNM #495848 (type).

Figures 3 - 5. *Nyssa* species

Figure 3. Small, slightly damaged, endocarp. Note longitudinal ridges. X 6. USNM #495849.

Figure 4. A second small endocarp, strongly damaged. X 6. USNM #495850.

Figure 5. Large endocarp. Note longitudinal ridges and faint trace of margin of valve on the upper left margin. X 4. USNM #495851.

Figures 6 - 8. *Symplocos grimsleyi* sp. nov.

Figure 6. Lateral view (apex up) of an endocarp with surficial ridges. X 4. USNM #495852 (type).

Figure 7. Lateral view (apex up) of second endocarp. X 4. USNM #495853.

Figure 8. Cross-section of endocarp with two mature locules (above), both containing seeds and one presumed aborted locule (below) containing lighter sediment. Note longitudinal ridges. X 12. USNM #495854.

Figures 9, 10. *Vitis* species #1

Figure 9. Dorsal view (apex up); the eroded face possesses an elongate chalazal knot; a dorsal groove runs from the apex to the base. X 5.5. USNM #495859.

Figure 10. Ventral view (apex up); The infolds are narrow and parallel, with a faint central groove marking the path of the raphe. X 5.5. USNM #495859.

Figures 11, 12. *Vitis* species #2

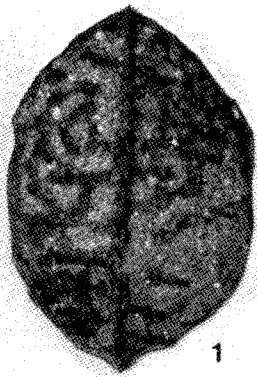
Figure 11. Dorsal view (apex up). The apex has a pronounced beak. The arched surface is smooth, with a large chalazal knot and a weak chalaza-apex groove. The raphe makes a positive ridge around the base of the seed. The seed surface is smooth. X 8. USNM #495860.

Figure 12. Ventral view (apex up). The infolds are parallel. A small groove indicates the path of the raphe. X 8. USNM #495860.

Figures 13, 14. *Ampelopsis* species

Figure 13. Dorsal view (apex up). The apex has a mildly pronounced beak. The strongly arched surface bears a central chalazal knot; the raphe creates a positive ridge around the base of the seed. There is no dorsal groove. Note radial striations. X 9. USNM #495861.

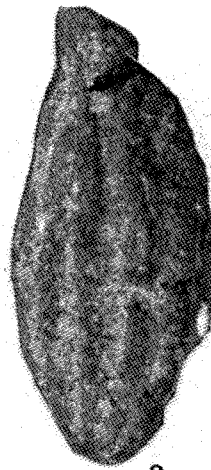
Figure 14. Ventral view (apex up). The ventral infolds are divergent. The raphe forms a positive ridge over the ventral surface leading to the apical beak. X 9. USNM #495861.



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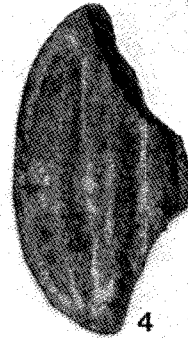
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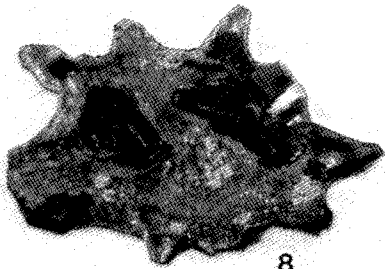
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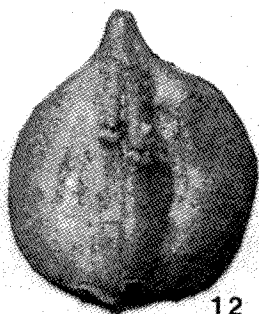
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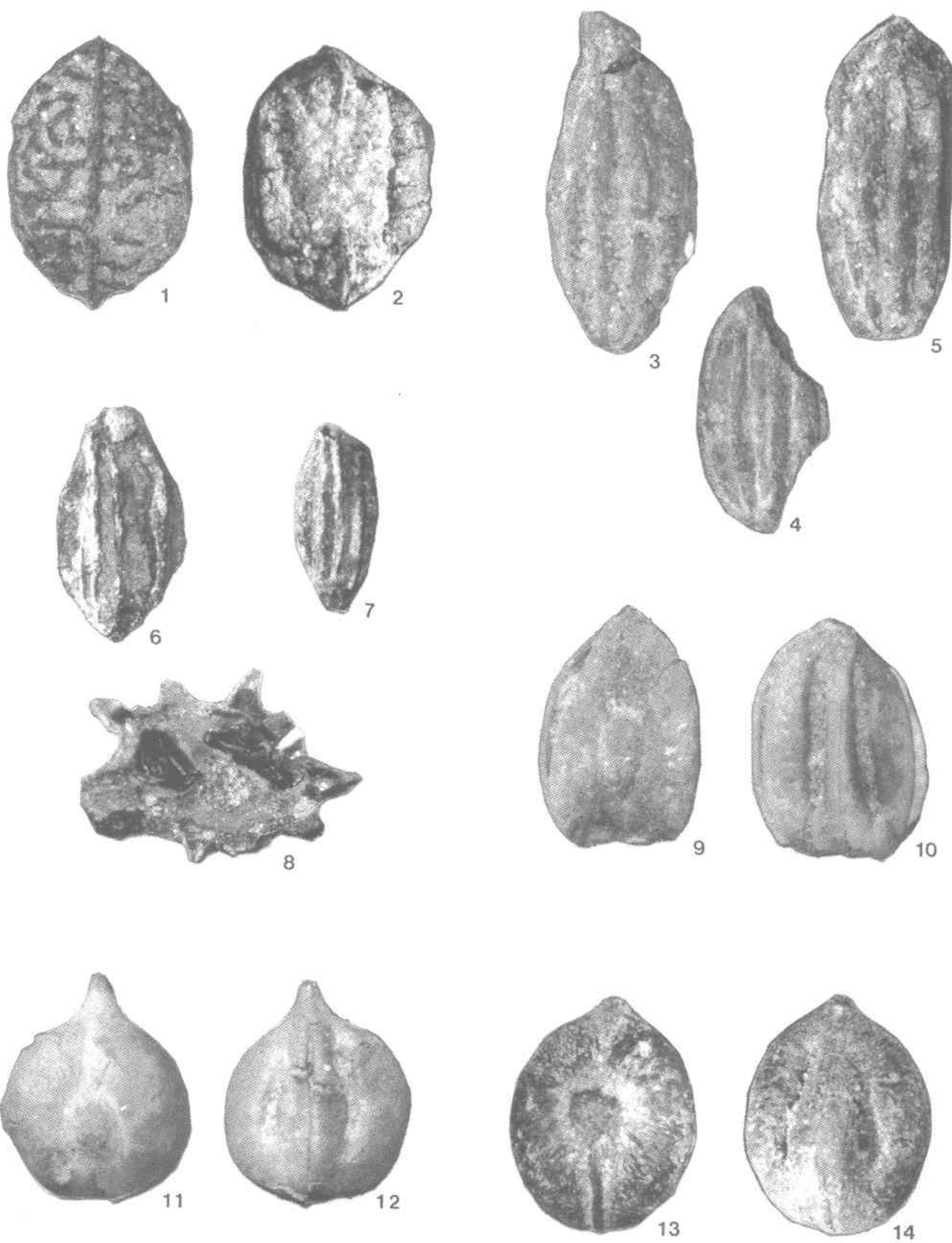
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**PLATE 3****Figures 1, 2. Unknown angiosperm #1**

Figure 1. Dorsal view of one specimen, note small protuberances occasionally uniting to make ridges on the arched surface. X 10. USNM #495862.

Figure 2. Ventral view of the second specimen. The two ventral faces are flat, meeting at a central line which appears to be the point of dehiscence. X 10. USNM #495863.

**Figures 3 - 6. Unknown angiosperm #2**

Figures 3, 4. Lateral view of the two fruits, the left intact, the right broken on its base. Note the faint longitudinal ridge on the left fruit indicating possible site of dehiscence, and the finely spaced latitudinal striations on the corresponding ridge on the right hand fruit. X 6.5. USNM #495864 (Fig. 3) USNM #495865 (Fig. 4).

Figures 5, 6. Apical view of the two fruits. Note the eight longitudinal ridges. The right hand fruit (corresponding to figure 4) clearly exhibits two "stigmatic" lobes, bisected by the line of the longitudinal dehiscence. X 6.5. USNM #495864 (Fig. 5) USNM #495865 (Fig. 6).

**Figure 7. Unknown object #1**

Lateral view of what is most likely a concretion closely mimicking a spherical fruit. X 7. USNM #495866.

**Figure 8. Unknown object #2**

Lateral view of a flattened lenticular object which may be a piece of water worn wood, or less likely, a large seed or fruit. X 1.8. USNM #495867.

**Figures 9, 10. *Nypa* cf. *burtini* (Brogniart) Ettingshausen**

Figure 9. Endocarp in matrix (right) adjacent to an uneroded fruit of living *Nypa fructicans* (left). The surface of the living fruit is the outer exocarp, while the exocarp has been eroded from the fossil to reveal the endocarp. Consequently, the intact fossil would have been larger. X 0.5.

Figure 10. Detail; the linear impressions of the exocarp fibers can be seen on the surface of the endocarp. X 0.8.



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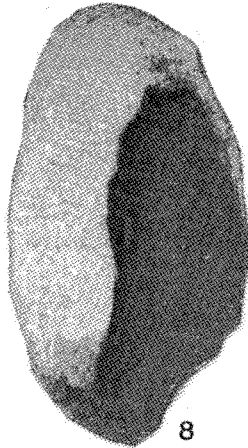
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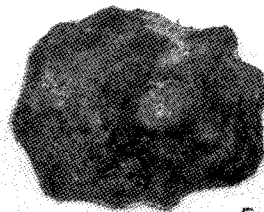
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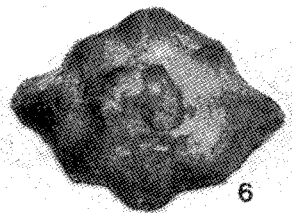
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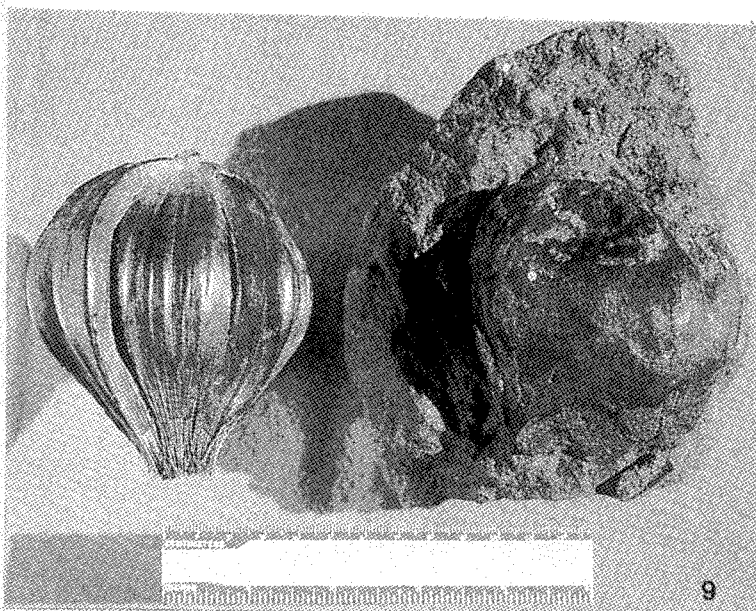
8



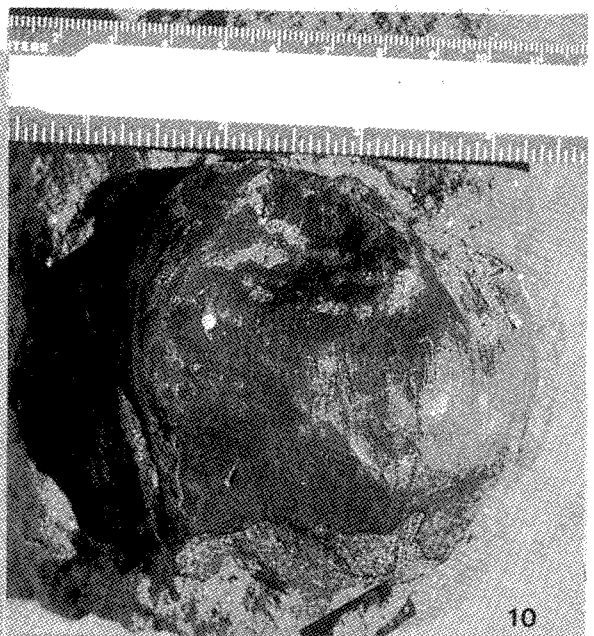
5



6



9



10

